DER ZOOLOGISCHE GARTEN

THE ZOOLOGICAL GARDEN

Zeitschrift für die gesamte Tiergärtnerei (Neue Folge)

Offizielles Organ des Verbandes der Zoologischen Gärten – VdZ
Organ of the World Association of Zoos and Aquariums – WAZA

ISSN 0044-5169
Zool. Garten N.F.
92 (2025) 2 · pp. 73-218

Volume 93
Issue 2 · 2025

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Verlag Natur & Wissenschaft · Solingen

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doi:10.53188/zg0042 Zool. Garten N.F. 93 (2025) 73-100 THE ZOOLOGICAL GARDEN

Analyse der globalen Haltungs- und Zuchtbedingungen von Klunkerkranichen (*Bugeranus carunculatus*) zur Verbesserung des Reproduktionserfolgs

Analysis of the global husbandry and breeding conditions of wattled cranes (*Bugeranus carunculatus*) to improve reproductive success

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Zusammenfassung

Aufgrund zunehmender hydrologischer Eingriffe und Störungen durch Menschen sowie Verbuschung von Feuchtgebieten gehen geeignete Habitate für die in Afrika beheimateten Klunkerkraniche (*Bugeranus carunculatus*) immer mehr zurück. Um das Überleben dieser bedrohten Vogelart sicherzustellen, werden diese Tiere weltweit in menschlicher Obhut gezüchtet. Da Klunkerkraniche unter allen Kranicharten die niedrigste Fortpflanzungsrate haben und in Haltung besonders schwer zu züchten sind, sollten in dieser Arbeit mögliche Ursachen für den geringen Zuchterfolg identifiziert werden. Dafür wurde mittels eines Fragebogens versucht, Haltungs- und Zuchtbedingungen der gesamten ex-situ-Population weltweit zu erfassen und Zusammenhänge zwischen diesen Bedingungen und der Reproduktionsrate zu analysieren.

Letztendlich flossen die Daten von 130 Individuen in die Statistiken ein, von denen sich 70 in Paarhaltung befanden. Die Gehegegröße hatte weder Einfluss auf Aggressivität noch auf das reproduktive Verhalten. Es konnte keine eindeutige Auswirkung des Vorhandenseins von Gewässern im Gehege auf das Wohlbefinden und den Zuchterfolg nachgewiesen werden. Handaufgezogene Tiere, männliche Tiere und Tiere mit Besucherexposition waren signifikant aggressiver. Harmonisches Paarverhalten konnte nur bei den Tieren nicht beobachtet werden, die mit 27 Jahren oder älter verpaart wurden. Harmonisches Paarverhalten korrelierte nicht mit der Länge der Partnerschaft.

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Geschlechtsreife Weibchen legten ausschließlich Eier, wenn sie sich in Paarhaltung oder in Nachbarschaft zu anderen Kranichen befanden. Weibchen, die aggressives Verhalten innerhalb des Paares erfuhren, legten signifikant häufiger keine Eier. Harmonisches Paarverhalten und keinerlei Aggressivität innerhalb des Paares waren absolut notwendige Kriterien für befruchtete Eier. Die Annahme, dass sich eine Handaufzucht negativ auf den Reproduktionserfolg auswirkt, konnte bei männlichen Tieren bestätigt werden. Diese brachten signifikant weniger befruchtete Eier hervor und es fehlte jeglicher Nachweis von Nachkommen. Die Hypothese, dass flugfähige Männchen mehr befruchtete Eier hervorbrachten als kupierte oder beschnittene Männchen, konnte nicht bestätigt werden. Es wurde allerdings deutlich, dass kupierte Männchen im Alter über 20 Jahre seltener befruchtete Eier hervorbrachten. Zunehmendes Alter hatte einen positiven Einfluss auf die Eifürsorge.

Aus den Ergebnissen ließ sich folgern, dass Handaufzuchten insbesondere bei männlichen Klunkerkranichen im Sinne des Tierwohls, des Reproduktionserfolgs und der Sicherheit der Tierpfleger zu vermeiden sind. Eine kostümierte Aufzucht unter strengen Richtlinien und frühzeitige Sozialisierung mit Artgenossen kann einer Fehlprägung entgegenwirken.

Eine Neuverpaarung ist angeraten, wenn es keinerlei paarbindendes Verhalten gibt, wenn ein Paar aggressiv zueinander ist oder wenn einer der Partner auf Menschen fehlgeprägt ist. Vom Kupieren der Flügel ist besonders bei Männchen abzuraten, da dieser irreversible Eingriff auch eine Verkürzung der natürlichen Reproduktionsphase mit sich bringt und künstliche Besamung bei Klunkerkranichen eine anspruchsvolle Methode ist, die mit viel Stress für die Tiere und hohem Personalaufwand einhergeht.

Schlüsselwörter: Klunkerkranich, Haltungsbedingungen, Zuchtprogramm, EEP

Einleitung

Ökologie und Verbreitung

Der Klunkerkranich (*Bugeranus carunculatus*) gehört zur Familie der Kraniche und wird in EAZA-Institutionen als ein EEP geführt. Der Klunkerkranich kommt ausschließlich in Afrika vor und ist unter allen afrikanischen Kranicharten am engsten an Feuchtgebiete gebunden. Seine Hauptnahrungsquelle besteht aus aquatischen Wurzeln, Knollen und Gräsern. Zwar gehören auch Amphibien, Insekten, Mollusken und kleine Vertebraten zu seinen Nahrungsquellen, doch der Anteil von pflanzlicher Nahrung ist beim Klunkerkranich von allen Kranichen am größten. Regionale Wanderungen zur Nahrungssuche erfolgen abhängig von saisonalen Regenzeiten und Überflutungen (Aticho et al., 2018; Morrison, 2019; Urban et al., 1986).

Klunkerkraniche sind die größten Kraniche Afrikas und kommen nur noch in drei voneinander isolierten Populationen vor, die zusammen den Weltbestand von etwas über 9.600 Individuen ausmachen (Morrison, 2019). Aktuell ist die Art von der IUCN als gefährdet (vulnerable) eingestuft (The IUCN Red List of Threatened Species, 2018) und im Washingtoner Artenschutzabkommen im CITES Appendix II gelistet (Checklist of CITES Species for *Bugeranus carunculatus*, o. J.).

Trotz der geografischen Nähe ist die südafrikanische Population genetisch von der Hauptpopulation im Süden Zentralafrikas isoliert. Die klimatischen Unterschiede und die deutlich weitere Entfernung voneinander machen daher auch eine genetische Isolation der äthiopischen Population sehr wahrscheinlich (Jones et al., 2006).

Zirka 75 % der Weltpopulation kommen in bestimmten Schlüsselgebieten im südlichen Zentralafrika vor. Zu diesen gehören die Kafue-Schwemmebenen im Süden Sambias, die Einzugs-

gebiete des Sambesi im Westen Sambias und dessen Delta in Mosambik, das Okavango Delta in Botswana und die Bangeweulubecken im Norden Sambias (Morrison, 2019).

Die Brutzeit von Klunkerkranichen beginnt im südlichen Zentralafrika zum Ende der Trockenzeit. Die darauffolgenden Überschwemmungen werden genutzt, um Nester aus Pflanzenmaterial und Schlamm im Wasser zu bauen. Klunkerkraniche haben von allen afrikanischen Kranicharten mit 33-36 Tagen die längste Inkubationszeit (Prange, 2016, S. 116), die niedrigste Gelegegröße (durchschn. 1,4 Eier/Gelege) und die längste Aufzuchtzeit (ca. 135 Tage) (Prange, 2016, S. 114). Das zweite Ei eines Geleges dient – falls es überhaupt gelegt wird – nur zur Sicherheit bei Verlust oder Zerstörung des ersten Eies, ist deutlich kleiner und enthält weniger Dotter. Nach Schlupf des ersten Kükens wird das zweite Ei zurückgelassen, bevor es schlüpft (Archibald & Lewis, 1996, S. 23; Wattled Cranes Recovery Program, o. J.).

Gefährdung und Schutz

Für die Bewässerung von landwirtschaftlichen Flächen, den Betrieb von Wasserkraftwerken und die Wasserversorgung der Bevölkerung werden in Afrika zunehmend Flüsse umgeleitet und Dämme errichtet. Davon betroffen sind unter anderem die Kafue-Schwemmebenen und der Cubango beziehungsweise Okavango Fluss in Angola und Botswana, der das Okavango-Delta – ein Binnendelta in Botswana – speist (Mendelsohn, 2021).

Durch solche hydrologischen Eingriffe wird nicht nur die verfügbare Wassermenge flussabwärts der Dämme reduziert, die die Feuchtgebiete aufrechterhalten soll. Es werden auch die saisonalen Schwankungen des Wasserstands ausgehebelt, die Antrieb für Wanderungen und Fortpflanzungsrhythmen der Klunkerkraniche sind (Harris & Mirande, 2013). In normalen Jahren brüten zum Beispiel an den Kafue-Schwemmebenen in Sambia 40 % aller Klunkerkranich-Paare. In Jahren mit reduzierter Überflutung hingegen nur 3% (Urban et al., 1986). Die Reproduktion kann grundsätzlich das ganze Jahr über stattfinden, ist aber in den unterschiedlichen Verbreitungsgebieten an die saisonalen Regenfälle angepasst (Beilfuss, 2002; Lifka, 2008; Mirande et al., 1996).

Weitere Herausforderungen für den Erhalt von Klunkerkranichen sind laut Shanungu et al. (2015) abnehmende Reproduktionsraten wegen des Verlusts von geeigneten Lebens- und Bruträumen, unter anderem aufgrund von Störungen durch Menschen und Verbuschung. Diese wird insbesondere durch die Ausbreitung invasiver Arten wie *Mimosa pigra* vorangetrieben (Blaser, 2013; Kamweneshe et al., 2003). Hinzu kommen Verluste von Eiern, Nestern und Küken durch Brände und menschliche Einflüsse wie Vergiftung, Jagd, Verzehr, Handel oder Zerstörung von Eiern oder andere Tötungen von Tieren (Morrison, 2019).

In Südafrika werden die zweiten Eier der Gelege eingesammelt, in menschlicher Obhut aufgezogen und wieder ausgewildert, um die südafrikanische Population zu stärken (Gene Pool Security – KZN Crane Foundation, o. J.). Für die Hauptpopulation und die äthiopische Population gibt es bislang keine Auswilderungsprojekte.

All diese Faktoren haben trotz der Etablierung zahlreicher Schutzgebiete und kontrollierter Jagdgebiete im Habitat der Klunkerkraniche sowie des genannten Auswilderungsprojektes dazu geführt, dass der Bestand von 16.000 Tieren um 1980 auf aktuell etwa 9.600 Tiere zurückging. Da besonders in Botswana und Angola die Errichtung weiterer Dämme geplant ist, ist davon auszugehen, dass die wilden Populationen in Zukunft weiter abnehmen werden (Kaul & Lawrence, 2024; Mendelsohn, 2021). Stabile und gesunde ex-situ-Populationen von Klunkerkranichen in zoologischen Gärten und privaten Einrichtungen stellen daher eine von vielen Notwendigkeiten dar, um den Fortbestand dieser Art sicherzustellen (Smith et al., 2011).

Ex-situ-Situation

Um einen intakten Zuchtbestand in menschlicher Obhut zu ermöglichen, müssen die wesentlichen Faktoren für eine zuverlässige Reproduktion bekannt sein. Bedingungen in Haltung unterscheiden sich bezüglich der meisten Faktoren stark von der Wildbahn (Hawkins, 2010; Mirande et al., 1997). Welche davon maßgeblich für eine artgerechte Unterbringung sind, ist bei Klunkerkranichen noch nicht vollständig verstanden und soll in dieser Arbeit weiter untersucht werden.

Unter den Kranichen ist der Klunkerkranich aufgrund seiner Sensibilität und geringen Fortpflanzungsrate besonders schwer in menschlicher Obhut zu züchten (del Hoyo et al., 1996, S. 84; Lifka, 2008, S. 31). Den Ansprüchen der Art in zoologischen Gärten gerecht zu werden, ist die zentrale Herausforderung im Management der ex-situ-Populationen.

Zwar sind Schutz vor Fressfeinden und ausreichendes Nahrungsangebot vermeintliche Vorteile des Lebens in menschlicher Obhut, doch fehlt es oft an einer freien Partnerwahl, einer störungsfreien, dem Habitat ähnlichen Umgebung und der Möglichkeit für natürliches Verhalten wie Nahrungssuche und freie Fortbewegung (Newberry, 1995; Rozendaal, 2024). Hinzu kommen die potenziellen Einflüsse von Klima, Fütterung, Aufzucht und Prägung jedes einzelnen Vogels (Ellis et al., 1996).

Paare reagieren besonders in der Brutzeit anfällig auf Störungen und können bei Stress aggressives Verhalten gegenüber Tierpflegern, Besuchern und, im Falle von Vergesellschaftung, anderen Tieren zeigen. Im natürlichen Habitat wird zirka 1 km^2 um das Nest herum von einem Paar verteidigt, wobei das gesamte Territorium über 16 km^2 groß sein kann (McCann & Benn, 2006). Bei Haltung in Paaren kann die Aggression auch am Partner ausgelebt werden (L. Fuller, 2024, persönliche Kommunikation) und sogar bis zur Tötung des Partners führen (Mirande et al., 1997).

Gee (1983) berichtet, dass Kraniche, die sich für Reproduktion und Ausstellung in Haltung befinden, sowohl auf Artgenossen geprägt sein müssen als auch eine Gewöhnung an Menschen im Juvenilstadium erfahren sollten. Letzteres dient der Verminderung von Stress und dadurch der langfristigen Reduktion des Kortisolspiegels im Blut, welcher den Reproduktionszyklus der Kraniche stören kann. Die Art der Aufzucht sollte für jedes Individuum an das Ziel der Haltung angepasst sein (Wellington et al., 1996). Bei Tieren in einem Auswilderungsprogramm ist daher anders vorzugehen als bei solchen, die zur Zucht in Haltung bleiben sollen. In jedem Fall sollte die Fehlprägung auf Menschen bei Handaufzuchten vermieden werden, da Menschen sonst als Artgenossen und somit als potenzielle Partner oder Konkurrenten angesehen werden. Solche Individuen erleben dann mehr Stress durch menschliche Nähe und können hochaggressiv und gefährlich für Menschen sein (Swengel et al., 1996).

Besonders bei großen Vögeln ist es gängige Praxis, Flügel zu kupieren oder zu beschneiden, um aufwändige Übernetzungen der meist großen Gehege zu vermeiden (Tyson, 2014). Bei Untersuchungen an Mandschurenkranichen haben Paare mit beschnittenen oder kupierten Männchen deutlich weniger befruchtete Eier hervorgebracht (Brown et al., 2019). Ob die Flugfähigkeit des Männchens auch bei Klunkerkranichen ein Faktor für die erfolgreiche Kopulation ist, ist noch nicht eindeutig belegt. Das Kupieren von Flügeln, bei dem zur lebenslangen Flugunfähigkeit ein Teil der Hand amputiert wird, ist mittlerweile in vielen Ländern inklusive Deutschlands verboten (§6 Absatz 1 des Tierschutzgesetzes).

Darüber hinaus ist zu klären, ob die Bindung des Reproduktionszyklus‘ an Niederschlag und Tageslänge eine Anpassung an begrenzte Nahrungsverfügbarkeit und Feindschutz in situ ist oder ob diese auch bei Haltung in anderen Breitgeraden und Klimazonen beibehalten wird. Neben Tageslänge und Temperatur ist nach Brown (1988) die Anwesenheit eines geschlechtsreifen Männchens ein entscheidender Faktor für die Eiproduktion bei vielen Wildvögeln. Brown

(2017) konnte durch Untersuchungen bei Schreikranichen in Haltung einen positiven Effekt von Gewässern im Gehege auf den Östrogenspiegel des Weibchens sowie die Produktion und Fertilität von Eiern nachweisen. Ob dieser Zusammenhang auch bei Klunkerkranichen besteht, ist bisher nicht geklärt, es lässt sich aufgrund der Bindung an Wasser im natürlichen Habitat aber mutmaßen. Lifka (2008) empfiehlt für Klunkerkraniche die Haltung in Gehegen mit natürlichem Teich.

Untersuchungen der International Crane Foundation zeigen zudem, dass die Gehegegestaltung allgemein bei Kranichen einen signifikanten Einfluss auf die Eiproduktion hat (Mirande et al., 1997).

Ziel der Arbeit

Anhand des bisherigen Wissens über Klunkerkraniche in Haltung und ihrem natürlichen Habitat sowie den Erkenntnissen durch Untersuchungen an anderen Kranicharten in Haltung sollen mögliche Ursachen für die niedrige ex-situ-Reproduktionsrate herausgefunden werden. Ob es ein Stadium in der Brut gibt, in dem ein Großteil der Paare scheitert und welcher Schritt von der Balz über die Paarung, Eiablage und Inkubation bis hin zum Schlupf und der Aufzucht des Kükens nicht erfolgreich abläuft, soll in dieser Arbeit geklärt werden.

Auf der Informationsgrundlage von erfolgreichen Brutpaaren sollen mögliche Störfaktoren identifiziert werden und Maßnahmen zur Verbesserung des Wohlbefindens und des Bruterfolgs der Klunkerkraniche gefunden werden. Dabei werden Alter, Aufzuchttyp, Flügelstatus der Männchen, Gehegegestaltung, Störung durch Besucher, Tierpfleger und andere Tiere, Interaktion der Partner und Paarbindung sowie Klima als Einflussfaktoren betrachtet.

Das Maß an Stress eines Tiers wird anhand von aggressivem Verhalten gemessen. Neben der Übersicht über den globalen Reproduktionserfolg sollte explizit untersucht werden, ob flugfähige Männchen zu mehr befruchteten Eiern führen.

Außerdem ist die Hypothese zu prüfen, ob größere, der Natur nachempfundene Gehege und Haltung ohne Exposition zu Besuchern oder anderen Kranichen Stress und Territorialverhalten reduzieren und ob die Tiere sich dadurch häufiger paaren, mehr befruchtete Eier hervorbringen und diese zuverlässiger inkubieren.

Darüber hinaus soll die Hypothese untersucht werden, ob eine Handaufzucht durch ein erhöhtes Stress-Level und mögliche Fehlprägung auf Menschen einen negativen Effekt auf den Reproduktionserfolg hat.

Material und Methoden

In dieser Arbeit wurde das generische Maskulinum gleichermaßen für weibliche und männliche Personenbezeichnungen verwendet, um die Lesbarkeit zu erleichtern.

Institutionen und Kontakte

Für eine möglichst große Stichprobe und aussagekräftige Ergebnisse zu erhalten, war es das Ziel, jedes Tier, das sich aktuell in menschlicher Obhut befindet, in die Analyse miteinzubeziehen. Zunächst wurde mit dem Zoological Information and Management System (ZIMS) „species360“ eine Liste aller Institutionen erstellt, die Klunkerkraniche halten und ZIMS benutzen. Die erste Kontaktaufnahme mit EAZA-Institutionen sowie dem internationalen Zuchtbuchführer Frederick Beall erfolgte durch Bernd Marcordes, EAZA-Zuchtbuchführer für Klunkerkraniche. Frederick Beall stellte Kontaktdaten von Institutionen der Association of Zoos and Aqua-

riums (AZA) in Nordamerika und regionalen Zuchtbuchführern von Südafrika, Japan, China und Taiwan zur Verfügung. Außerdem wurden weitere Institutionen über die Zootierliste (www.zootierliste.de) gesucht. Über das online zugängliche Internationale Zuchtbuch (Stand 2022) wurden alle weiteren Tiere privaten Züchtern zugeordnet. Deren Kontaktdaten wurden über Suchmaschinen, ZIMS, oder private Kontakte der Mitarbeiter des Zoologischen Garten Kölns herausgefunden.

Fragebogen

Über einen einheitlichen Fragebogen wurden demografische Daten, Details zu Aggressivität, Aufzuchttyp, Flugfähigkeit, Gehegeausstattung und -größe, Vergesellschaftung und Besucherexposition für jedes Individuum erhoben. Zur Untersuchung der Anpassung des Legeverhaltens an Klima und Aufenthaltsort wurden bei weiblichen Tieren die Legetermine festgehalten. Im Falle von Paarhaltung wurde harmonisches und reproduktives Verhalten sowie Aggressivität untereinander und Bruterfolg erfragt. Es wurden größtenteils geschlossene Fragen gestellt, um die statistische Auswertung der Antworten zu erleichtern und mit einem möglichst geringen Zeitaufwand die Antwortrate der Institutionen zu erhöhen. Der Fragebogen wurde Zoodirektoren, Kuratoren oder Tierpflegern übermittelt, um eine fachkundige Einschätzung der Tiere zu erhalten.

Datentransformation und Auswertung

Um die Legedaten der Weibchen auf verschiedenen Hemisphären vergleichbar zu machen, wurden diese in Relation zum Monat mit der niedrigsten Tageslichtdauer gesetzt. Es wurde der zeitliche Abstand (in Monaten) zum Monat M_i mit dem kürzesten Tag der jeweiligen Hemisphäre gemessen (M_N = Dezember, M_S = Juni). Legedaten, die zeitlich vor dem jeweiligen Bezugsmonat lagen, wurden als Negativwerte festgehalten.

Jeder Institution wurde basierend auf den Informationen der Webseite klimatabelle.de (Klimatabelle und Klima weltweit, o. J.) eine Klimazone und über gpskoordinaten.de (GPS Koordinaten, o. J.) ein Breitengrad zugeordnet.

Die Analyse des reproduktiven Verhaltens erfolgte schrittweise nach den erforderlichen Stadien für eine erfolgreiche Brut:

- Kompatibilität und Balz eines Paares
- Fruchtbarkeit der Eier
- Legeverhalten und Nestbau
- Inkubation
- Schlupf
- Aufzucht des Kükens

Anzumerken ist, dass zum Untersuchungszeitpunkt in den Institutionen der AZA aus Kapazitätsmangel keine Zuchtempfehlung vorlag und teilweise befruchtete Eier entfernt wurden.

Jedem Paar wurde das höchste von ihm erreichte Brutstadium zugeordnet, das heißt ein der Gruppe *n* zugeordnetes Paar hat ebenfalls alle Stadien $<n$ erreicht.

Einige Institutionen gaben auf Nachfrage an, saisonale Überflutungen während der Brutzeit mit Sprenklern, Gartenschläuchen oder überlaufenden Pools zu simulieren. Um den Einfluss dieses Faktors auswerten zu können, hätten unter anderem Daten zu natürlichen Regenzeiten, Niederschlagsmengen und Bodenbeschaffenheit hinzugezogen werden müssen. Daher wurde auf die Analyse des Mikroklimas im Gehege verzichtet.

Mithilfe von RStudio (Version 2024.09.1+394) wurde die statistische Auswertung durchgeführt und sämtliche Abbildungen mit den Paketen „ggplot2“ und „RColorBrewer“ erstellt.

Wenn nicht explizit genannt, wurde für alle Testergebnisse ein Signifikanzniveau von 5 % zugrunde gelegt. Es wurden robuste Tests für kleine Stichproben ausgewählt.

Ergebnisse

Globale Übersicht

Insgesamt flossen Daten von 130 Klunkerkranichen in 35 Institutionen aus elf verschiedenen Ländern in Europa, Nordamerika, Afrika und Asien in die Untersuchung ein. Davon waren 62 männlich (45,6 %), 71 weiblich (52,2 %) und drei unbekannten Geschlechts (2,2 %). Die Altersspanne lag bei 0 bis 56 Jahren mit einem Median von 14 Jahren. Die Altersverteilung unterschied sich auf den Kontinenten nicht signifikant voneinander.

70 Tiere wurden als Paar gehalten, woraus sich insgesamt 35 Paare ergaben. Die übrigen Individuen befanden sich in Einzelhaltung oder in Gruppen, wobei letzteres nur für neun Klunkerkraniche der Fall war. Diese waren immatur oder in gleichgeschlechtlichen Gruppen. Insgesamt waren 19 Klunkerkraniche mit anderen Tierarten vergesellschaftet. Darunter waren diverse Gänsevögel (Anseriformes), Störche (Ciconiiformes) und Huftiere (Artiodactyla). Ein Weibchen wurde unter anderem mit einem Afrikanischen Strauß (*Struthio camelus*) zusammen gehalten.

Von allen Institutionen weltweit lag nur in den Zoologischen Gärten der AZA keine Zuchtempfehlung vor. Für den Erhalt der Population wurden hier pro Brutsaison drei der befruchteten Eier zum Schlupf gebracht und alle weiteren zerstört (Beall, 2024, persönliche Kommunikation). Aus den insgesamt 35 Paaren gingen in der Brutsaison 2024 fünf Jungtiere hervor [0,14 Küken/(Brutpaar*Brutsaison)].

Die Gehege waren zwischen 30 m^2 und 40.000 m^2 groß und hatten mit einer Ausnahme alle über 50 % natürlichen Boden. Es gab 29 beschnittene, 34 kupierte und 60 flugfähige Vögel. Fünf weitere Tiere waren wegen körperlicher Einschränkungen nicht mehr flugfähig.

Physiologische Grundlagen

In der Brutsaison 2024 war das jüngste eierlegende Weibchen fünf Jahre und das älteste 40 Jahre alt. Die Recherchen der Stammbäume aller Klunkerkraniche über ZIMS ergab ebenfalls ein Alter von fünf Jahren für die erste erfolgreiche Reproduktion bei Weibchen überhaupt. Männchen reproduzierten sich den Daten der Stammbäume nach bereits im Alter von drei Jahren.

Laut dem internationalen Zuchtbuch (Stand 2022) war das Höchstalter bei der letzten Reproduktion von Weibchen 46 und von Männchen 44 Jahre. Das durchschnittliche Alter der letzten Reproduktion lag bei beiden Geschlechtern bei zirka 20 Jahren.

Aggressivität

Aggressives Verhalten gegenüber Tierpflegern lag zwischen 0 und 10 mit einem Median von 0 und einem Mittelwert von 2,3. Kein Vogel unter fünf Jahren zeigte Aggressivität und im Spearman-Korrelationstest konnte ein moderater und signifikant positiver Zusammenhang der Aggressivität zum Alter festgestellt werden (p-Wert <0,01; $\rho = 0{,}42$). Dieselbe Testung für Tiere ab fünf Jahren war nicht signifikant (p-Wert = 0,15). Alle weiteren Einflussfaktoren auf die Aggressivität wurden nur anhand der potenziell geschlechtsreifen Tiere untersucht. Die Ergebnisse sind Tabelle 1 zu entnehmen.

Tab. 1: Testergebnisse der Aggressivität gegenüber Tierpflegern als abhängige metrische Variable. Außer Alter (*) wurde jeder Faktor nur für potenziell geschlechtsreife Tiere getestet.
Tab. 1: Test results for aggressiveness towards animal keepers as a dependent metric variable. Except for age (*) each factor was only tested for potentially sexually mature animals.

unabhängige Variable	p-Wert	Effektstärke	Test
Alter*	<0,001	ρ=0,42	Spearman-Korrelationstest
Aufzuchttyp	<0,05		Kruskal-Wallis Test
Geschlecht	<0,05		Mann-Whitney-U Test
Gehegegröße	0,58	ρ=-0,06	Spearman-Korrelationstest
Besucherexposition	0,07		Mann-Whitney-U Test
Saison	<0,01		Mann-Whitney-U Test
Aggressivität gegenüber Besuchern	<0,001	ρ=0,48	Spearman-Korrelationstest
Aggressivität gegenüber Kranichen	0,89	ρ=-0,02	Spearman-Korrelationstest

Die Aggressivität gegenüber Tierpflegern korrelierte moderat positiv und hoch signifikant mit der Aggressivität gegenüber Besuchern. Die Gehegegröße sowie die Aggressivität gegenüber benachbarten Kranichen korrelierten nicht mit dem Maß der Aggressivität gegenüber Tierpflegern. Männliche Tiere waren signifikant aggressiver gegenüber Tierpflegern als weibliche. Die gleiche Tendenz zeigten Tiere mit Besucherexposition, jedoch knapp nicht signifikant (p-Wert = 0,07).

Es wurde ein signifikanter Zusammenhang zwischen Aufzuchttyp und der Saison, also dem Zeitraum, wann ein Tier aggressiv war, festgestellt. Die unterschiedlichen Verteilungen sind Tabelle 2 zu entnehmen.

Tab. 2: Anzahl der Individuen, die nie, nur in der Brutsaison oder ganzjährig aggressiv gegenüber Tierpflegern waren, eingeteilt nach deren Aufzuchttyp.
Tab. 2: Number of individuals that were never, only during the breeding season or year-round aggressive towards animal keepers, categorized by their type of rearing.

Aufzuchttyp	Nie	In Brutsaison	ganzjährig
Handaufzucht	8	4	13
Kostümaufzucht	7	2	7
Pflegeelternaufzucht	5	5	0
Elternaufzucht	28	8	7
Unbekannte Aufzucht	7	1	5

Die Mehrheit der handaufgezogenen Tiere (13 von 25) war ganzjährig aggressiv gegenüber Tierpflegern, während unter Elternaufzuchten nur sieben von 43 Individuen ganzjährig aggressiv waren. Klunkerkraniche, die nur während der Brutzeit Aggressivität zeigten, waren signifikant weniger aggressiv als solche, die das ganze Jahr über aggressiv waren. Dies galt für beide Geschlechter.

Per Kruskal-Wallis Test wurde ein signifikanter Einfluss des Aufzuchttyps auf das Maß der Aggressivität bestätigt. Diese wird in Abbildung 1 dargestellt.

Handaufgezogene Tiere waren signifikant aggressiver als Elternaufzuchten (p-Wert<0,01) und etwas aggressiver als Pflegeelternaufzuchten (p-Wert=0,08). Kostümaufzuchten unterschieden sich nur von Elternaufzuchten signifikant durch höhere Aggressivität. Tiere unbekannter Aufzucht unterschieden sich von keinem Aufzuchttyp hinsichtlich der Aggressivität gegenüber Tierpflegern.

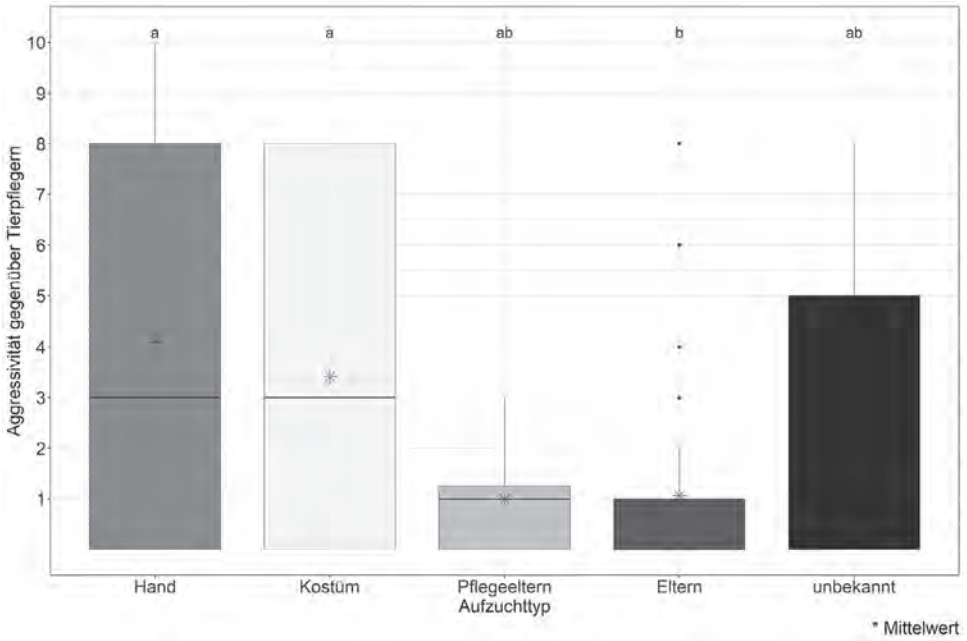

Abb. 1: Boxplot-Diagramm zur Darstellung von Aggressivität gegenüber Tierpflegern auf einer Skala von 0-10 auf der y-Achse abhängig von Aufzuchttyp auf der x-Achse (n = 124).
Fig. 1: Boxplot diagram showing aggressiveness towards animal caretakers on a scale of 0-10 on the y-axis depending on the rearing type on the x-axis (n = 124).

Die hohe Aggressivität von Handaufzuchten deckt sich mit den Erfahrungen mehrerer Kuratoren weltweit und den Angaben von Frederick Beall (2024, persönliche Kommunikation). Das Zuchtprogramm von Klunkerkranichen der AZA-Institutionen in Nordamerika legt – diesen Erfahrungen entsprechend – größten Wert auf die Elternaufzucht von geschlüpften Küken, um Fehlprägungen und hohe Aggressivität zu vermeiden.

71 Individuen lebten neben anderen Kranichen in benachbarten Gehegen. Das Maß an Aggressivität diesen gegenüber lag zwischen 0 und 8, mit einem Median von 0, Mittelwert von 0,82 und hing weder signifikant mit der Haltungsform, dem Geschlecht, der Aufzuchtart noch der Gehegegröße zusammen. Allein bei Tieren mit Besucherexposition trat eine hochsignifikant höhere Aggressivität gegenüber benachbarten Kranichen auf (p-Wert <0,01).

Aggressivität zwischen vergesellschafteten Tieren wurde vom Fragebogen nicht abgedeckt. Es wurde aber in einem Fall davon berichtet, dass es regelmäßig zu aggressivem Verhalten zwischen einem Klunkerkranich und einem Afrikanischen Strauß kam.

Der Einfluss von Versteckmöglichkeiten im Gehege wurde nicht mit Hilfe von schließender Statistik ausgewertet. 76 Klunkerkraniche waren Besuchern nicht exponiert. Bei den Tieren außerhalb des Besucherbereichs wurde ein gewisses Maß an Ruhe und Rückzugsmöglichkeiten vorausgesetzt. Von 51 Individuen mit Besucherexposition hatten nur vier keine Versteckmöglichkeit oder Sichtschutz im Gehege. Darunter waren zwei einzelne Tiere, die 0/10 und 1/10 aggressiv waren sowie ein moderat aggressives Paar, das ein fertiles Ei gelegt und inkubiert hatte, nachdem es erst seit 2024 zusammen gehalten wurde. Alle vier Tiere waren Eltern- oder Pflegeelternaufzuchten. Die Gehege waren zwischen 54 und 558 m^2 groß.

Reproduktives Verhalten

Von den insgesamt 112 potenziell geschlechtsreifen Individuen hatten sich 37 bereits in Haltung reproduziert (33 %). Für die folgenden Ergebnisse wurden nur potenziell geschlechtsreife Individuen in Paarhaltung betrachtet, also Paare, in denen das Männchen mindestens drei Jahre und das Weibchen mindestens fünf Jahre alt war.

In Abbildung 2 ist zur Übersicht dargestellt, wie viele Paare in den Brutsaisons 2023 und 2024 welches Stadium der Reproduktion erreichten. Wenn ein Paar ein Stadium erreicht hat, impliziert dies auch, dass das Paar alle vorherigen Stadien erfolgreich durchlaufen hat. Alle Paare werden also nur in der Kategorie des fortgeschrittensten Stadiums aufgeführt.

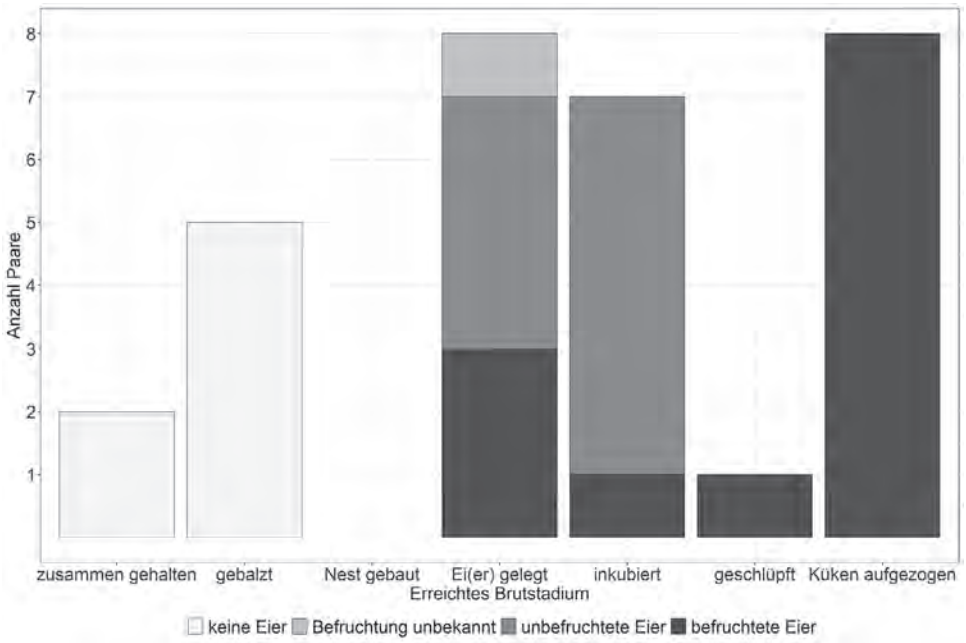

Abb. 2: Übersicht des erreichten Brutstadiums und Fruchtbarkeit der Eier aller potenziell geschlechtsreifen Paare in der Brutsaison 2023 und 2024 (n = 31).

Fig. 2: Overview of the achieved breeding stage and fertility of the eggs of all potentially sexually mature pairs in the 2023 and 2024 breeding seasons (n = 31).

Zwei Paare zeigten keinerlei paarbindendes Verhalten, fünf Paare hatten gebalzt aber kein Nest gebaut, kein Paar hatte ein Nest gebaut, ohne Eier zu legen. Acht Paare hatten Eier gelegt, aber nicht zuverlässig inkubiert. Von diesen waren die Eier von vier Paaren unbefruchtet. Sieben Paare inkubierten ihre Eier zuverlässig, ohne dass es zum Schlupf kam, bei einem Paar waren Küken geschlüpft, aber verstorben, und acht Paare hatten erfolgreich Küken aufgezogen.

Unter den Paaren, die gebalzt hatten, ohne ein Nest zu bauen oder Eier zu legen, waren nur Weibchen zwischen fünf und acht Jahren, Weibchen, die 40 Jahre oder älter waren, oder Paare, bei denen es zu aggressivem Verhalten untereinander kam.

Kompatibilität der Paare

Ob und wie häufig gemeinsames Rufen und Tanzen auftrat, wurde als leitendes Kriterium für hohe Harmonie und Kompatibilität innerhalb eines Paares herangezogen. Dem gegenüber stand aggressives Verhalten unter den Partnern als Zeichen für schlechte Harmonie und niedrige Kompatibilität.

In den Untersuchungen korrelierte die Häufigkeit des paarbindenden Verhaltens weder mit dem Alter der einzelnen Individuen noch mit der Dauer der Partnerschaft. Keinerlei paarbindendes Verhalten trat allerdings nur bei geschlechtsreifen Klunkerkranichen auf, die erst mit 27 Jahren oder älter mit ihrem aktuellen Partner zusammengeführt wurden. Paarbindendes Verhalten war signifikant häufiger bei Klunkerkranichen, die seit jungem Alter im aktuellen Paar lebten.

Es konnte kein eindeutiger Zusammenhang zwischen der Altersdifferenz und der Harmonie eines Paares festgestellt werden. Ob ein Paar miteinander rief und tanzte, war unabhängig von deren Aufzuchttyp. Allerdings korrelierte die Aggressivität gegenüber Tierpflegern bei Weibchen hochsignifikant und moderat positiv mit der Häufigkeit des Rufens und Tanzens (p-Wert <0,01; $\rho = 0,5$). Bei Männchen zeigte sich dieser Zusammenhang nicht.

Ob harmonisches Paarverhalten auftrat, hatte bei Weibchen keinerlei Zusammenhang mit der Aggressivität gegenüber Tierpflegern, Besuchern oder anderen Kranichen. Bei Männchen, die aggressiv gegenüber 1. Tierpflegern oder 2. anderen Kranichen waren, trat häufiger kein paarbindendes Verhalten auf. Dies war allerdings nicht signifikant (1.: p-Wert = 0,12; $\rho = -0,39$ und 2.: p-Wert = 0,1; $\rho = -0,52$).

Innerhalb eines Paares trat Aggressivität in vier von 35 Fällen auf. Es gab statistisch keinen Hinweis darauf, dass die Aggressivität innerhalb eines Paares mit dem Alter der Individuen, der Länge der Paarhaltung, der Gehegegröße oder Aggressivität gegenüber den Tierpflegern zusammenhing. Keines der vier Paare hatte andere Kraniche in Nachbarschaft. Drei der vier Paare befanden sich in Gehegen mit Besucherexposition. Die Hälfte der betroffenen Weibchen und drei der vier betroffenen Männchen waren handaufgezogen, ohne dass hier ein signifikanter Einfluss nachgewiesen werden konnte. Nur ein Weibchen in diesen vier Paaren hatte in der Brutsaison 2024 ein Ei gelegt. Dieses war nicht befruchtet.

Nestbau und Legeverhalten

Von insgesamt 59 Weibchen im Alter von fünf Jahren oder älter legten 35 Weibchen Eier. Dabei hatte die Haltung in Paaren einen hochsignifikant positiven Einfluss auf das Eierlegen im Vergleich zu Einzel- oder Gruppenhaltung. Weibchen in Paarhaltung legten allerdings signifikant weniger Eier, wenn es gelegentlich zu Aggressivität innerhalb des Paares kam.

Andere Kraniche in Nachbargehegen hatten einen positiven Einfluss auf das Legeverhalten von Weibchen in Einzelhaltung, jedoch ohne Signifikanz (p-Wert=0,1). Alle acht einzelnen Weibchen, die Eier legten, lebten in benachbarten Gehegen zu anderen Kranichen.

Die Weibchen in Einzelhaltung legten weniger Eier, wenn sich Gewässer jeglicher Art in ihrem Gehege befanden. In Paarhaltung hatten Gewässer keinen Einfluss auf das Legeverhalten.

Von 23 Paaren, die Nester gebaut hatten, kam es bei 22 zur Eiablage. Der Ort des Nests hing hochsignifikant von der Beschaffenheit des Gewässers ab (p-Wert<0,01). Die entsprechenden Verteilung ist in Tabelle 3 aufgeführt. Der Großteil der Nester wurde auf solidem Grund gebaut, einzig bei natürlichen Gewässern im Gehege wurden drei von vier Nestern am Gewässerufer oder im Wasser errichtet.

Tab. 3: Neststandort abhängig von Gewässerbeschaffenheit im Gehege (n = 22).
Tab. 3: Nest location depending on water quality in the enclosure (n = 22).

Neststandort	Betoniertes Gewässer	Natürliches Gewässer	Wanne	Kein Gewässer
Boden	13	1	0	3
Gewässer/Ufer	2	3	0	-

Es konnte ein gewisser Zusammenhang zwischen den Legedaten der Weibchen und dem Klima festgestellt werden. Die Beträge der Breitengrade korrelierten leicht positiv mit dem Legebeginn der Weibchen, jedoch ohne Signifikanz (p-Wert=0,16; =0,25). Für die Analyse des Legeendes wurden die Legedaten der Weibchen in AZA-Institutionen außer Acht gelassen. Das Legeende korrelierte moderat positiv und signifikant mit dem Betrag des Breitengrads (=0,5). Der Legebeginn der Weibchen innerhalb einer Institution variierte teilweise um mehrere Monate. Laut Marcordes (2024, persönliche Kommunikation) hat jedes Weibchen feste Legedaten, die kaum variieren. Die Legedaten eines Weibchens wurden bei diesen Untersuchungen nicht beachtet, da es 2024 im September auf der Nordhalbkugel erstmals ein Ei gelegt hatte. Laut Mirande et al. (1996) kann es große Unterschiede zwischen dem ersten und den folgenden Legejahren eines Weibchens geben und die Legesaison startet über die ersten drei Legejahre immer früher.

Fruchtbarkeit der Eier

In keiner der Institutionen, in denen Paare nur unbefruchtete Eier legten, wurde in den Brutsaisons 2023 und 2024 eine künstliche Besamung durchgeführt. Befruchtete Eier gab es bei Paaren, die seit null Jahren bis hin zu 15 Jahren gemeinsam gehalten wurden. Befruchtete Eier kamen bei Weibchen bis zum Alter von 29 und bei Männchen bis zum Alter von 32 Jahren vor.

Das Alter des Weibchens hatte in der logistischen Regression nach Firth einen signifikant negativen Zusammenhang mit der Fruchtbarkeit der Eier. Nur eins der acht Weibchen, die über 20 Jahre alt waren, hatte ein befruchtetes Ei gelegt. Das Alter der Männchen hatte keinen derartigen Zusammenhang.

Die Aufzuchtart der verpaarten Männchen hatte einen signifikanten Zusammenhang mit der Fruchtbarkeit der Eier. Bei Elternaufzuchten waren fünf von acht Eiern befruchtet und bei Pflegeelternaufzuchten fünf von fünf, während bei Kostümaufzuchten eins von vier und bei Handaufzuchten null von drei Eiern befruchtet waren. Der Effekt der Aufzuchtart der Weibchen war hingegen nicht signifikant (p-Wert = 0,63). Die prozentuale Fertilität der Eier abhängig vom Aufzuchttyp beider Geschlechter ist Tabelle 4 zu entnehmen.

Tab. 4: Anteil der befruchteten Eier abhängig von Aufzuchttyp und Geschlecht (n, Männchen = 23; n, Weibchen = 23).
Tab. 4: Proportion of fertilized eggs depending on rearing type and sex (n, males = 23; n, females = 23).

Aufzuchttyp	Prozentuale Fertilität der Eier bei Männchen [%]	Prozentuale Fertilität der Eier bei Weibchen [%]
Handaufzucht	0	33
Kostümaufzucht	25	50
Pflegeelternaufzucht	100	100
Elternaufzucht	63	63
Unbekannte Aufzucht	67	100

Die Flugfähigkeit der Männchen in einem Paar zeigte für die Fertilität der Eier keine Signifikanz. Insbesondere konnte kein Unterschied zwischen dem Effekt von kupierten und beschnittenen Flügeln fest gestellt werden, obwohl bei kupierten Kranichmännchen eine erschwerte Kopulation diskutiert wird (Strehlow, 2021). Um auszuschließen, dass ein Nachteil der Flugunfähigkeit bei Männchen durch Alter und Erfahrung des Männchens ausgewogen werden konnte, wurde auch dieser Faktor geprüft. Statistisch lag für die Interaktion von Alter und Flügelstatus keine Signifikanz in der logistischen Regression vor (p-Wert = 0,35; Koeffizient = -0,26).

Allerdings traten bei kupierten Männchen unbefruchtete Eier signifikant häufiger in höherem Alter auf (Koeffizient = -0,15). In Abbildung 3 ist zu sehen, dass sich sowohl bei fliegenden als auch bei beschnittenen Männchen das Alter der Männchen nicht abhängig von der Fertilität der Eier unterscheidet.

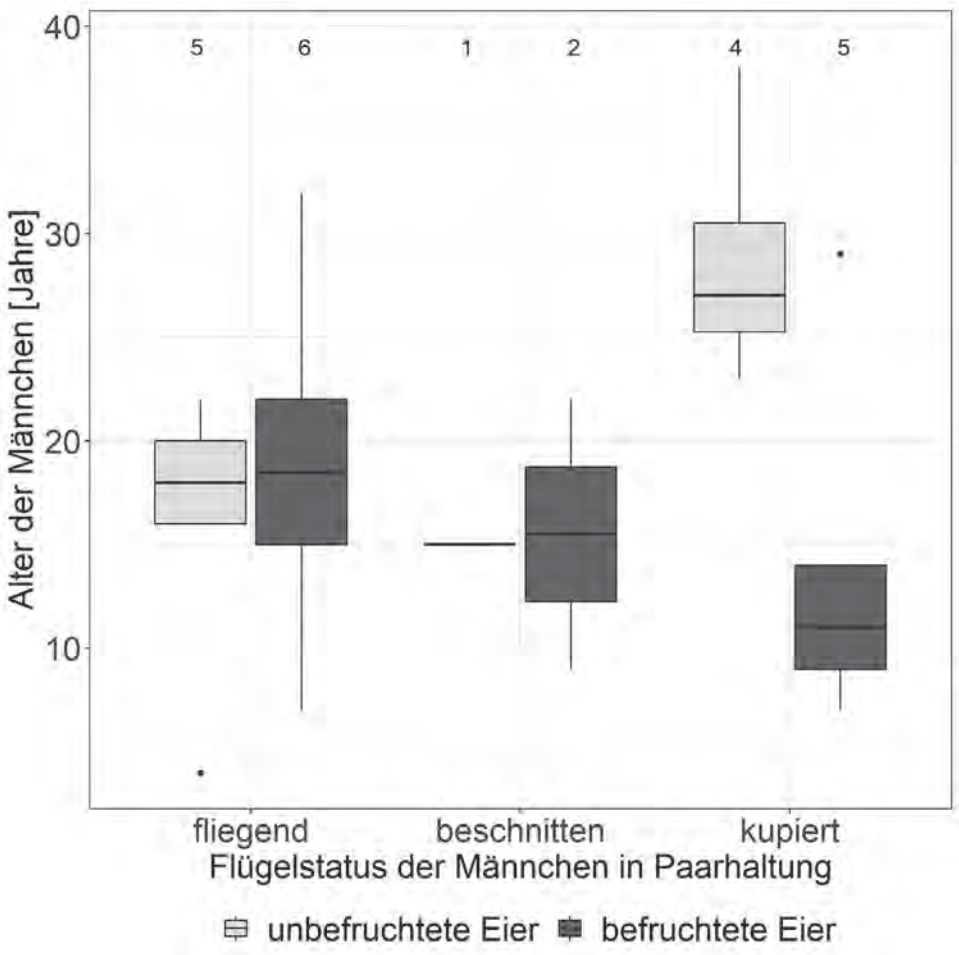

Abb. 3: Alter der Männchen auf der y-Achse in Jahren und Flügelstatus auf der x-Achse, unterteilt nach Fruchtbarkeit der Eier (n=23).

Fig. 3: Male age in years on the y-axis and wing status on the x-axis, categorized by egg fertility (n=23).

Die Beschaffenheit des Gewässers im Gehege hatte insofern einen Einfluss auf die Fruchtbarkeit, dass vier von vier Paaren mit natürlichem Gewässer und nur sieben von 14 Paaren mit betoniertem Gewässer befruchtete Eier hatten. Hier lag keine Signifikanz vor (p-Wert = 0,16).

Bei Betrachtung der einzelnen Fälle fiel auf, dass die drei kupierten Männchen der vier Paare mit natürlichem Gewässer maximal 14 Jahre alt waren, während kupierte Männchen in Paarhaltung mit betoniertem Gewässer im Median 26,6 Jahre alt waren.

Es konnte festgestellt werden, dass Eier tendenziell eher befruchtet waren, wenn Weibchen in jungem Alter verpaart wurden. Dieser Effekt war nicht signifikant (p-Wert = 0,14).

Kein Paar ohne harmonisches Verhalten hatte befruchtete Eier hervorgebracht.

In vier Fällen wurde von geschlechtsreifen Paaren berichtet, die oft miteinander riefen und tanzten, Eier legten, sie zuverlässig inkubierten, aber diese nie befruchtet waren. Die Paare waren seit sechs bis 14 Jahren zusammen und alle vier Männchen waren flugfähig. In ZIMS waren die letzten Einträge zum Geschlecht der Männchen 14 bis 20 Jahre her und es wurde die Möglichkeit einer homosexuellen Verpaarung mit den Institutionen diskutiert. Bei allen vier vermeintlichen Männchen wurden erneute Geschlechtsbestimmungen geplant, deren Ergebnisse zum Ende dieser Untersuchung noch ausstanden.

Fürsorge für Eier und Inkubation

Es lagen zu 20 Paaren Informationen zur Eifürsorge vor. Fünf Paare hatten Eier gelegt, ohne diese zu inkubieren. Darunter fielen die Paare, in denen einer der Partner die Eier zerstörte, Eier nicht adäquat gegen andere Tiere im Gehege verteidigt wurden, Eier verschwanden oder schlichtweg nicht bebrütet wurden. Ein Paar hatte in der Vergangenheit gute Eifürsorge gezeigt, aber die Eier wurden direkt nach dem Legen durch die Tierpfleger entfernt. Bei Paaren, in denen ein Partner die Eier nach der Eiablage zerstörte, konnte auch für den anderen Partner keine gute Eifürsorge festgehalten werden. Mit einer Ausnahme hatten in allen weiteren Paaren je beide Partner eine gute Eifürsorge gezeigt. Unter den sieben Paaren, die Küken aufgezogen hatten, zeigte ein Partner keine gute Eifürsorge. Dort wurde auf eine kombinierte Inkubation zurückgegriffen. Im Schlupf wurde das Küken dem Paar zurückgeführt und von diesen gut versorgt.

Weder Aufzuchtart, Geschlecht, Besucherexposition noch Vergesellschaftung mit anderen Tieren hatten statistisch einen Einfluss auf die Fürsorge für Eier. Als signifikant negativ zeigte sich der Einfluss von Aggressivität gegenüber anderen Kranichen (Koeffizient = -0,49). Eine gute Eifürsorge hing hingegen positiv mit der Aggressivität gegenüber Tierpflegern zusammen, jedoch knapp ohne Signifikanz (p-Wert = 0,08; Koeffizient = 0,22).

Die Größe des Geheges hatte keinen Einfluss auf die Eifürsorge. Der positive Einfluss von Alter auf die Eifürsorge war knapp nicht signifikant (p-Wert = 0,06; Koeffizient = 0,09).

Schlupf und Aufzucht

Weltweit gab es nur eine Institution mit einem Paar, bei dem über mehrere Brutsaisons Küken schlüpften, aber diese bald darauf starben. Neurologische Defizite und Nährstoffmangel wurden als augenscheinliche Ursache dafür angegeben.

Die erfolgreiche Aufzucht von Jungtieren konnte in den Brutsaisons 2023 und 2024 bei acht Paaren beobachtet werden, die seit vier bis 15 Jahren gemeinsam gehalten wurden. Die Männchen befanden sich vom ersten bis 26. Lebensjahr in ihrem Brutpaar und die Weibchen vom ersten bis 15. Lebensjahr. Die Männchen waren zwischen sieben und 32 und die Weibchen zwischen sieben und 29 Jahre alt. Von den acht Männchen dieser Paare war keines handaufgezogen. Keins der reproduktiven Paare war mit anderen Tierarten im Gehege vergesellschaftet.

Die Gehege waren 175-360 m² groß und drei von acht Paaren waren Besuchern exponiert. Alle acht Paare bekamen als Hauptfutter Kranichpellets.

Für jedes Individuum in Paarhaltung wurde über Stammbaumrecherchen in ZIMS festgehalten, ob es jemals Nachkommen hervorgebracht hatte. Der Aufzuchttyp von Männchen hing mit dem Nachweis von Nachkommen zusammen, jedoch knapp ohne Signifikanz (p-Wert = 0,07). Bei Weibchen bestand hier kein Zusammenhang. In Abbildung 4 sind die Häufigkeiten von Nachkommen abhängig vom Aufzuchttyp für beide Geschlechter dargestellt. Unter allen Männchen (Abbildung 4 links) gab es kein handaufgezogenes Individuum mit Nachkommen. Bei Weibchen (Abbildung 4 rechts) war der Nachweis von Nachkommen abhängig von der Aufzuchtart sehr ausgeglichen.

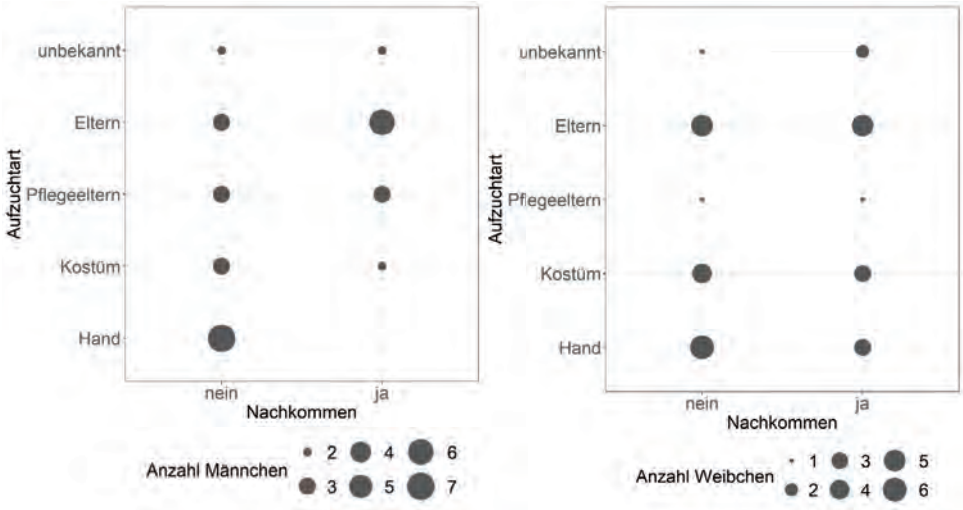

Abb. 4: Blasendiagramme zur Häufigkeitsdarstellung von Tieren mit Nachkommen abhängig von ihrer Aufzuchtart; links: potenziell geschlechtsreife Männchen in Paarhaltung, rechts: potenziell geschlechtsreife Weibchen in Paarhaltung.

Fig. 4: Bubble charts showing the frequency of animals with offspring depending on how they are reared; on the left: potentially sexually mature males housed in pairs, on the right: potentially sexually mature females housed in pairs.

Diskussion

Kontaktaufnahme

Die internationale Kommunikation per E-Mail war in vielen Fällen bei der ersten Kontaktaufnahme erschwert, da E-Mails nicht zustellbar waren oder vermutlich lange unbemerkt blieben. Über persönliche Kontakte der Mitarbeiter des Kölner Zoos und anderer Institutionen konnte ein schriftlicher Austausch in vielen Fällen ermöglicht werden. Die Hilfsbereitschaft und Vernetzung der Mitarbeiter von Zoologischen Gärten und privaten Züchtern untereinander trug enorm zur Reichweite und Antwortrate auf den erstellten Fragebogen bei. Oft konnte der Erstkontakt über private Textnachrichten oder Anrufe etabliert werden. Die Motivation, Klunkerkraniche besser zu verstehen und schützen zu können,

schien viele Kuratoren und Tierpfleger dazu zu bewegen, umfassende Informationen über ihre Tiere zu teilen.

Aus dem asiatischen Raum konnten nur wenige Informationen zusammengetragen werden was sich mit den Erfahrungen von Frederick Beall und Bernd Marcordes deckte. Womöglich besteht kein Bedarf nach Austausch und Zusammenarbeit oder durch technische, sprachliche oder politische Hindernisse misslang die Kommunikation.

In jedem Fall war Zeitmangel ein Faktor, der sich entscheidend auf die Antwortrate auswirkte. Um möglichst viele Halter zur Teilnahme an der Untersuchung zu bewegen, war Hartnäckigkeit, Flexibilität und Geduld gefragt. Einige Fragebögen wurden telefonisch, per Videokonferenz oder bei persönlichen Treffen geklärt.

Ein Großteil der Ergebnisse basierte auf den Daten, die über den Fragebogen erhoben wurden. Besonders die skalierten Fragen unterlagen einer subjektiven Einschätzung. Für jeden Fragebogen wurde vorausgesetzt, dass die Fragen sorgfältig durchgelesen und korrekt beantwortet wurden und durch Formatierungsänderungen oder technische Störungen keine Antworten fehlerhaft waren. Falls Antworten nicht plausibel waren oder den Informationen aus ZIMS oder dem internationalen Zuchtbuch widersprachen, wurden diese Informationslücken nach Möglichkeit in weiteren Kontakten geschlossen.

Da sehr viele Faktoren erhoben wurden und die Stichprobe recht klein war, wurde nur in wenigen Fällen die Interaktion von Variablen untersucht, um zuverlässige und stabile Ergebnisse zu erhalten. Die Überlegungen, zum Beispiel mehrere potenzielle Stressoren zu einer Variablen zusammenzufassen, wurden verworfen. Die Faktoren Besucherexposition, Fütterung durch Tierpfleger und Kraniche in Nachbarschaft unterschieden sich massiv in Dauer, Art und Effekt der Störung.

Übersicht und Grundlagen

Das Geschlechterverhältnis innerhalb der Kontinente war sehr ausgeglichen, sodass zumindest theoretisch ein großer Anteil an Verpaarungen möglich wäre.

Klunkerkraniche können sich auch mit über 40 Jahren noch reproduzieren. Dass laut internationalem Zuchtbuch (Stand 2022) die letzte Reproduktion beider Geschlechter allerdings durchschnittlich schon mit zirka 20 Jahren erfolgte, zeigte ein großes Potenzial für ein besseres Management.

Bei Vergesellschaftung mit anderen Tierarten sollte auf eine gute Verträglichkeit und die Möglichkeit einer störungsfreien Brut geachtet werden. Die Haltung mit großen Huftierherden könnte dem im Wege stehen. Von Vergesellschaftung, bei der es zu Aggressivität zwischen den Tieren kommt, ist abzuraten, um dauerhaften Stress zu vermeiden.

Aggressives Verhalten

Vorweg ist anzumerken, dass neben Aggressivität auch übermäßige Gefiederpflege, Fluchtversuche oder Unterwürfigkeit ein Zeichen von Stress sein können (Swengel et al., 1996). In den Untersuchungen wurde lediglich die Aggressivität als Maß für Stress erhoben. Zwar sollte für eine validere Analyse jedes Symptom von Stress betrachtet werden, doch wurde diese globale Befragung auf die Aggressivität als offensichtlichstes und objektivierbarstes Verhalten begrenzt.

Dass aggressives Verhalten nur bei Tieren ab fünf Jahren auftrat, lässt sich mit hormonellen Veränderungen erklären, die mit der Geschlechtsreife eintreten. Bei Gefahrensituationen im Habitat übernimmt das Männchen meist die Rolle des Verteidigers, während das Weibchen sich der Brut zuwendet (Mirande et al., 1997). Diese natürliche Aufgabenteilung erklärt, warum Männchen auch in Haltung signifikant aggressiver waren als Weibchen.

Dass größere Gehege nicht mit weniger Aggressivität gegenüber Tierpflegern verbunden waren, kann verschiedene Gründe haben. Die meisten Gehege waren unter 600 m^2 groß, was die Fläche der natürlichen Territorien weit untertrifft. In dieser Größenordnung ist das Maß an Territorialverhalten des Kranichs wahrscheinlich eher abhängig vom Individuum und Geschlecht. Bei deutlich größeren Anlagen wäre vermutlich weniger Aggression zu erwarten. Womöglich wurden aggressive Tiere aber auch in tendenziell größeren Gehegen gehalten, um ihnen eine Ausweichfläche in Stresssituationen zu bieten.

Bei Tieren, die ganzjährig hochaggressiv gegenüber Tierpflegern waren, ist eine Fehlprägung durch Handaufzucht wahrscheinlich. Der Stress durch menschliche Nähe bei diesen Tieren erklärte auch das aggressive Verhalten Besuchern gegenüber. Hier wäre eine Haltung ohne Besucherexposition ratsam. Viele Brutpaare wurden in einer ruhigeren und störungsfreieren Umgebung außerhalb des Besucherbereichs gehalten. Es gab allerdings auch einige Paare, die ohne jegliches Zeichen von Aggressivität im ausgestellten Bereich der Institutionen erfolgreich brüteten. Dies scheint eine Einzelfallentscheidung zu erfordern mit dem Blick auf höchstmögliches Wohlbefinden der Tiere und entsprechende Sicherheit der Tierpfleger.

Die hohe und ganzjährige Aggressivität vieler handaufgezogener Individuen fiel bei dem Austausch mit einigen Institutionen als schwerwiegendes Problem auf. Arbeiten im Gehege sind aufwendiger und die Sicherheit der Tierpfleger ist gefährdet, was zur zunehmenden Unbeliebtheit der Haltung von Klunkerkranichen führte. Dass sich insbesondere männliche Handaufzuchten seltener erfolgreich reproduzierten, spricht dafür, Handaufzuchten bei Klunkerkranichen möglichst zu vermeiden. Dies deckt sich mit den Erfahrungen von Frederick Beall, Bernd Marcordes und vielen Kuratoren. Falls keine Elterntiere oder Pflegeeltern zur Verfügung stehen, könnte die Nutzung eines Kostüms mit Klunkerkranich-Optik helfen, die Gewöhnung an Menschen zu reduzieren (*Protecting Cranes and the Places They Dance*, o. J.; Wellington et al., 1996).

In Abbildung 1 ist das Maß der Aggressivität von Kostümaufzuchten vergleichbar mit der von Handaufzuchten. Womöglich liegt das daran, dass die Aufzuchten per Kostüm unterschiedlich konsequent umgesetzt wurden. Der menschliche Kontakt mit dem Küken sollte nur sporadisch unkostümiert erfolgen und neben der optischen Isolation auch möglichst gesprächsfrei verlaufen (Nemutamvuni, 2024, persönliche Kommunikation; L. Fuller, 2024, persönliche Kommunikation, Duerr & Gage, 2020, S. 384–385). In der Zuchtfarm vom Johannesburger Zoo werden Küken im Auswilderungsprogramm ausschließlich von vollständig kostümierten Menschen aufgezogen. Tiere, die in Haltung bleiben sollen, werden dort von Menschen aufgezogen, die nur ihre Hand kostümieren (Nemutamvuni, 2024, persönliche Kommunikation).

Nach den Erfahrungen von van der Feesten (2025, persönliche Kommunikation) können sich auch aus Handaufzuchten zuverlässig brütende Tiere entwickeln. Vielleicht war der Vorteil dieser Zuchtfarm, dass die Jungvögel nur von einer Person versorgt wurden und sie seit dem Schlupf in Hörweite von Artgenossen waren. Ob diese Faktoren entscheidend zur Prägung der Küken beitragen, wäre ein interessanter Aspekt zukünftiger Untersuchungen. In zoologischen Gärten ist die Umgebung viel mehr von Menschen geprägt und es stehen weniger Tiere zur Artprägung für Jungvögel zur Verfügung.

Auch die akustische Prägung scheint bei einigen Kranicharten für späteres artspezifisches Verhalten und Balzen essenziell zu sein. Schreikraniche, die von Kanadakranichen aufgezogen wurden, wurden von ihrer eigenen Art wegen unterschiedlicher Lautäußerungen verstoßen (Duerr & Gage, 2020, S. 384). Ein negativer Einfluss von Pflegelternaufzuchten auf Klunkerkraniche für die artspezifische akustische Prägung konnte in dieser Untersuchung nicht bestätigt werden. Allerdings lagen auch keine genaueren Informationen darüber vor, ob die betroffenen Individuen von fremden Kranicharten oder von Klunkerkranichen aufgezogen worden waren. Darüber hinaus ist der negative Effekt von Pflegeelternaufzuchten in Haltung womöglich re-

duzierter, da keine freie Partnerwahl besteht und akustische Varianzen eher toleriert werden. Vielleicht hat die akustische Prägung bei Klunkerkranichen auch weniger Bedeutung als bei Schreikranichen oder die Jungvögel wurden früh genug mit Artgenossen sozialisiert.

Die Aufzucht und Prägephase sind für die Küken entscheidend (Duerr & Gage, 2020; Wellington et al., 1996). Die Aufzucht durch die eigenen Elterntiere oder Pflegeeltern mit gelegentlichem menschlichem Kontakt ist somit die wünschenswerteste Option für das spätere Tierwohl und den Bruterfolg der Tiere in Haltung. Laut Swengel et al. (1996) ist die sexuelle Prägung bei Kranichen von der früheren filialen Prägung zu differenzieren. Durch eine Sozialisierung mit Artgenossen im Alter von 30-45 Tagen könnten sexuelle Prägungen auf Menschen aufgehoben werden.

Dass keine Einflussfaktoren für das Maß an Aggressivität zu benachbarten Kranichen identifiziert werden konnten, legt die Vermutung nahe, dass dieses Verhalten individuell verschieden ist. Möglicherweise wurden die entscheidenden Faktoren dafür auch nicht erhoben. Es gab unterschiedliche Ansichten, ob ein Sichtschutz zwischen den Gehegen in diesen Fällen ausreichend wäre oder es eines gewissen Abstands der Gehege zueinander bedürfte. Laut Nemutamvuni (2024, persönliche Kommunikation) ist auch dies abhängig von den Individuen. In manchen Fällen sind Sichtschutze ausreichend, in anderen müssen die Klunkerkraniche in ein anderes Gehege gesetzt werden. Grundsätzlich gilt es, diesen dauerhaften Störfaktor vollständig zu unterbinden, um chronischen Stress zu vermeiden (Swengel et al., 1996). Es gab aber auch Paare, die sich erfolgreich reproduzierten, obwohl Aggressivität gegenüber benachbarten Kranichen dokumentiert wurde.

Reproduktives Verhalten

Das reproduktive Verhalten wurde anhand der potenziell geschlechtsreifen Tiere in Paarhaltung untersucht. Anzumerken ist dabei, dass die Geschlechtsreife auch später eintreten kann und Weibchen in Paarhaltung teilweise erst mit acht Jahren ihr erstes Ei legten.

Die Einteilung der Paare in erreichte Brutstadien erwies sich als gute Methode, um Ursachen von Misserfolgen bei der Reproduktion zu sehen. Diese ordinale Skala zeigte in Abbildung 2, dass die Hauptprobleme harmonische Paarbindung, Eiablage sowie zuverlässige Inkubation und Fruchtbarkeit der Eier waren.

Die Kompatibilität und Harmonie eines Paares ist ein absolut notwendiges Kriterium für eine erfolgreiche Zucht. Wenn möglich sollte ein Paar jung etabliert werden. Swengel et al. (1996, S. 114) geben zudem gleichaltrige Kraniche als geeigneter für eine Verpaarung an, damit das jüngere Individuum nicht eingeschüchtert von dem älteren Partner ist.

Harmonisches Paarverhalten korrelierte bei Weibchen positiv mit der Aggressivität gegenüber Tierpflegern, was zunächst verwunderlich war, da sich Männchen allgemein aggressiver verhielten. Da die Aggressivität gegenüber Tierpflegern bei handaufgezogenen Klunkerkranichen höher war, könnte dies auch bedeuten, dass der Aufzuchttyp des Weibchens in einem Paar weniger ins Gewicht fällt. Handaufgezogene Weibchen werden von Swengel et al. (1996, S. 225) als unterwürfiger beschrieben und lassen sich vermutlich eher erfolgreich verpaaren, während handaufgezogene Männchen wegen ihrer Dominanz und höheren Aggressivität häufiger einzeln gehalten werden mussten. Mirande et al. (1997) weisen darauf hin, dass hoch territoriales und gestresstes Verhalten von Männchen die Verletzungsgefahr beider Partner erhöht und dass die Ablenkung der Männchen einem gesunden Paarverhalten entgegenwirkt.

Die Paarbildung kann mehrere Wochen bis Monate in Anspruch nehmen und sollte von regelmäßigem gemeinsamem Rufen und Tanzen geprägt sein. Von Tieren, die zusammengehalten werden, aber niemals zusammen rufen und tanzen, sind keine befruchteten Eier zu erwarten. Dies gilt insbesondere auch für Tiere, die seit mehreren Jahren ohne Balz und Brutversuch in

einem Gehege koexistieren, da das harmonische Verhalten innerhalb eines Paares nicht positiv mit der Länge der Partnerschaft korrelierte. In diesen Fällen ist ein Partnerwechsel anzuraten. In einem Paar hatte ein Weibchen seit einem einmaligen Disput Angst vor seinem Partner. Dass selbst einmalige negative Ereignisse die Harmonie eines Paares langfristig schädigen können, spricht dafür, bei wiederholtem aggressivem Verhalten innerhalb eines Paares eine Neuverpaarung einzuleiten. Die betroffenen Paare waren größtenteils handaufgezogen und in Gehegen mit Besucherexposition. Die Projektion von Stress und Aggressivität auf den Partner wurde bereits von Mirande und Archibald (1990) beschrieben und dem könnte durch eine Haltung in einer störungsfreieren Umgebung vorgebeugt werden.

Die Haltung in Paaren zeigte sich für geschlechtsreife Weibchen als ausreichender Faktor für Eiproduktion. Einzig aggressives Verhalten innerhalb des Paares scheint dies zu hemmen. Innerhalb harmonischer Paare kommt es nicht zu aggressivem Verhalten.

Weibchen in Einzelhaltung legten ausschließlich Eier, wenn sich Kraniche in benachbarten Gehegen befanden. In diesen Fällen war von einer Verpaarung mit den benachbarten Kranichen auszugehen, wodurch die einzelnen Weibchen in Brutstimmung kamen. Die Kranichart schien hierbei nicht von Bedeutung zu sein. Es wurden bereits Hybride zwischen verschiedenen Kranicharten dokumentiert (Swengel et al., 1996, S. 118). Mit künstlicher Besamung könnten solche Nachbarschaften eine Methode sein, um auch befruchtete Eier von Weibchen in Einzelhaltung zu erhalten.

Den Legetermin eines Weibchens zu kennen, ist besonders in Fällen von künstlicher Besamung oder vorauszusehender schlechter Eifürsorge wichtig, da Klunkerkraniche teilweise nur ein Ei pro Brutsaison legen. Sofern eine Hand- oder Kostümaufzucht angestrebt wird, können Eier auch regelmäßig entfernt werden, ohne durch Kunsteier ersetzt zu werden. Einige Weibchen legen daraufhin ein weiteres Ei (Mirande et al., 1996). So könnte die Reproduktionsrate eines Paares künstlich erhöht werden, auch wenn dadurch die Möglichkeit der Elternaufzucht nur für eins der Küken bestünde.

Die Untersuchungen des Einflusses von Breitengrad und Klima auf das Legeverhalten hatten nur wenig Aussagekraft. Dass die Legeperiode in höheren Breitengraden später endete, deutet auf eine gewisse Anpassung an die absolute Tageslänge hin. Bei Betrachtung der einzelnen Daten unterschieden sich jedoch auch die Legedaten von Weibchen innerhalb einer Institution um mehrere Monate, sodass genetische oder individuelle Unterschiede womöglich ebenfalls von Bedeutung sind. Dass Weibchen in höheren Breitengraden und tieferen Minimaltemperaturen im Winter durchschnittlich später legten, deutet auf eine gewisse Anpassung an Klima und/oder Lichtexposition am Aufenthaltsort hin. Eine baldige Eiablage kündigt sich in der Regel mit Nestbau und gehäufter Balz an. Je nach Gehegegröße und -gestaltung kann ein errichtetes Nest aber auch von Tierpflegern unbemerkt bleiben oder sehr rudimentär ausfallen. Nach den Erfahrungen von van der Feesten (2025, persönliche Kommunikation) werden auch oft Eier gelegt und anschließend ein Nest drumherum gebaut. Mindestens vier Wochen vor dem Legebeginn der vorherigen Jahre sollte die künstliche Besamung bei einem Weibchen begonnen werden. Laut Gee (1983) eignet sich für die Prozedur ein Turnus von 3x/Woche. Künstliche Besamung erfordert qualifiziertes Personal und ist bei Klunkerkranichen besonders schwierig (van der Feesten, 2025, persönliche Kommunikation; Bremehr, 2025, persönliche Kommunikation; Lifka, 2008).

Dass sich die Tiere, die Tierpflegern gegenüber aggressiver waren, besser um ihre Eier kümmerten, weist auf ein natürliches Maß an Territorialverhalten hin. Zudem kommen Störungen durch Fütterungen in der Regel nur einmal am Tag vor, sodass dies das Brutgeschehen nicht zu sehr beeinträchtigt. Benachbarte Kraniche hingegen können einen permanenten Stressor darstellen und die Brutpaare maßgeblich vom Brüten abhalten (Swengel & Besser, 1996).

Es ist anzumerken, dass die Inkubation von Kranicheiern aufgrund ihrer Größe nicht ununterbrochen stattfinden muss. Elterntiere stehen häufig auf und Eier können ohne Probleme bis zu

einer Stunde nicht bebrütet werden ohne abzusterben (Urban et al., 1986). Dieser Zeitraum ist abhängig von Wetter und Außentemperaturen (Marcordes, 2024, persönliche Kommunikation; van der Feesten, 2024, persönliche Kommunikation). Manche Kuratoren interpretierten eine häufige Unterbrechung der Inkubation als schlechte Eifürsorge.

Grundsätzlich wird die adäquate Eifürsorge mit mehr Erfahrung besser, was den positiven Einfluss des Alters erklärt. Ein Problem, dass sich nicht beheben lässt, war die Neigung von mindestens zwei verpaarten Männchen und einem Weibchen, die Eier direkt nach dem Legen zu zerstören beziehungsweise zu fressen. Mirande et al. (1996) beschreiben dieses Verhalten als Zeichen von Stress. Nach der Einschätzung der Kuratoren ist dies eher eine Angewohnheit, die aus den zufälligen Erfahrungen des guten Geschmacks und der Nährstoffe von Eiern resultiert. Falls es gelingt, die Eier zur künstlichen Inkubation zu entnehmen und im Schlupf zurückzuführen, kann dieses Problem eventuell umgangen werden. Auch hierfür wäre es essenziell, den Legetermin des Weibchens abschätzen zu können. Manche Paare bemerken jedoch den Austausch durch Kunsteier und brechen den Brutversuch ab. Wenn der Zerstörung des Eis nicht vorgebeugt werden kann, wäre eine Neuverpaarung oder eine Trennung des Paares durch einen Zaun zu erwägen.

Wenn in Einzelfällen bei sehr harmonischen Paaren im geschlechtsreifen Alter nie Eier gefunden wurden, könnten diese entweder direkt nach dem Legen zerstört worden sein oder es sollte gegebenenfalls eine erneute Geschlechtsbestimmung des vermeintlichen Weibchens vorgenommen werden. Männliche Klunkerkraniche sind zwar oft etwas größer und schwerer als Weibchen, doch reicht die morphologische Inspektion nicht zur sicheren Geschlechtsbestimmung aus. Auch Chromosomenbestimmungen über Federproben können durch inkorrekte Durchführung oder Dokumentation fehlerhaft sein. Vögel können auch verwechselt worden sein, zum Beispiel wegen verlorener oder unleserlicher Ringe oder Transponder. Diese Möglichkeit zu prüfen, kann ebenfalls bei Paaren mit stets unbefruchteten Eiern lohnend sein, um auch da eine versehentliche homosexuelle Verpaarung auszuschließen.

Die geringe Fruchtbarkeit der Eier ist weltweit ein wesentlicher Faktor für die schlechte Reproduktionsrate von Klunkerkranichen. Handaufgezogene Männchen sind durch ihr oft erhöhtes Territorialverhalten so abgelenkt, dass sie nicht in Brutstimmung kommen oder nur sehr wenige Kopulationsversuche unternehmen. Gee (1983) weist auf die vergleichsweise niedrige Samenanzahl und -qualität bei Kranichen im Vergleich zu anderen Vögeln hin, was häufigere Paarungen erfordern würde. Daher fällt womöglich ein geringes Interesse von Männchen an der Reproduktion sehr ins Gewicht. Bei einer Fehlprägung auf Menschen ist eine natürliche Reproduktion mit Artgenossen ausgeschlossen, da diese nicht als potenzielle Partner angesehen werden (Gee, 1983).

Der Flügelstatus der Männchen schien nur bei kupierten Flügeln eine Rolle zu spielen. Auch Gee (1983) und Nicolich et al. (2001) erklären die hohe Unfruchtbarkeit von Kranichen in Haltung unter anderem mit kupierten Männchen. Lifka (2008) berichtet, dass sich die Balance bei der Kopulation bei diesen Tieren im Laufe der Jahre durch mehr Übung verbessert. Die aktuellen Untersuchungen zeigen hingegen einen negativen Effekt des Alters. Im jungen Alter sind die bis zu 1,85 m großen Männchen (Johnsgard, 1983, S. 121) durch gute körperliche Konstitution vermutlich noch in der Lage, für die Kopulation auf dem Weibchen stehend zu balancieren. Je älter und unbeweglicher die Kranichmännchen sind, umso unwahrscheinlicher wird bei kupierten Flügeln die erfolgreiche Befruchtung des Weibchens. Das älteste kupierte Männchen, das 2024 befruchtete Eier hervorgebrachte, war 21 Jahre alt. Da Kraniche in Haltung über 60 Jahre alt werden können (Mirande et al., 1996) und die Amputation der Hand eine lebenslange Flugunfähigkeit bedeutet, ist dieser Eingriff sehr sorgfältig abzuwägen. Insbesondere da Tiere häufig zwischen Institutionen getauscht werden und sich die Haltungsbedingungen in einem permanenten Wandel befinden, sollte die natürliche Reproduktionsfähigkeit der Männchen nicht

leichtfertig verkürzt werden. Künstliche Besamung stellt für die Tiere Stress und für die Tierpfleger eine schwierige und zeitintensive Alternative zur natürlichen Kopulation dar. Außerdem ist das alternative Beschneiden der Flügel mit weniger Kosten, Komplikationen und Schmerzen verbunden und zu alledem reversibel. Um die Balance der kupierten Männchen zu verbessern, empfehlen Swengel et al. (1996) und van der Feesten (2025, persönliche Kommunikation) bei Unfruchtbarkeit die Schwungfedern des intakten Flügels zu beschneiden.

Der positive Einfluss von natürlichen Gewässern auf die Fertilität der Eier konnte nicht sicher verifiziert werden. Der Datensatz enthielt die Daten von nur vier Paaren mit einem natürlichen Gewässer im Gehege und bei der Beurteilung der Fertilität von Paaren mit betoniertem Gewässer kamen konfundierende Variablen hinzu. Zum einen waren die kupierten Männchen hier älter, was als Faktor für erschwerte Kopulation identifiziert wurden. Zum anderen müssen betonierte Gewässer regelmäßig gereinigt werden, wodurch zusätzlicher Stress durch Betreten und Arbeiten im Gehege für die Klunkerkraniche entsteht. Ob das Mikroklima im Gehege einen positiven Effekt auf den Hormonspiegel des Weibchens haben kann, konnte nicht gezeigt werden. Dafür müssten neben der Gewässerbeschaffenheit die Niederschläge, Klimazone, die Bodenbeschaffenheit und Simulation von Überflutung mit betrachtet werden. Die Keimbelastung von natürlichen Gewässern dürfte besonders bei kleinen Gehegen mit mehreren Vögeln nicht zu unterschätzen sein. Laut Olsen et al. (1996) wird vermutet, dass Kranicharten besonders sensibel gegenüber Mykobakterien sind (*Mycobacterium avium*), die besonders bei Anlagen ohne Übernetzung leicht von Wildvögeln ins Gewässer eingetragen werden können.

Die persönliche Kommunikation mit der International Crane Foundation (Boardman, 2024) ergab, dass Kranichpaare natürliche Gewässer in der Regel nutzen, um am Ufer ihr Nest zu bauen, aber dass auch viele Brutpaare ohne Gewässer erfolgreich brüten. Die Wahl der drei von vier Paaren mit natürlichem Gewässer, ihr Nest direkt am Ufer oder im Wasser zu bauen, bestätigte diese Einschätzung und weist auf einen positiven Einfluss dieser Ausstattung hin. Ein Gehege ohne Gewässer steht in keinem Fall einer erfolgreichen Reproduktion im Weg. Fuller (2024, persönliche Kommunikation) weist auf den wichtigen Einfluss von Umgebungsfeuchtigkeit auf den Wasserverlust des Eis während der Inkubationszeit hin. Ein zu trockenes Klima im Nest könnte einer regelrechten Embryoentwicklung entgegenstehen. Die Dicke der Eischale wird vor allem vom Calciumgehalt des Futters bestimmt und ist maßgeblich für die Verdunstung von Wasser aus dem Ei. Bei den Paaren, deren befruchtete Eier regelmäßig absterben, könnte sowohl der Calciumgehalt des Futters wie auch der Neststandort eine Rolle spielen. Für diesen Aspekt wären weitere Untersuchungen des Futters und des Klimas im Gehege sinnvoll.

Brown et al. (2019) geben an, dass die Fruchtbarkeit von Eiern bei Schreikranichen bei näher verwandten Partnern abnimmt. Dadurch, dass sich unter den ohnehin schon wenigen Klunkerkranichen in menschlicher Obhut nur wenige reproduzieren, ist von einer recht hohen Verwandtschaft unter den Tieren auszugehen. Aus einzelnen Brutpaaren, die verlässlich züchten, gehen viele Nachkommen einer Blutlinie hervor, die möglichst nicht mehr miteinander verpaart werden sollten. Dieses Problem wird verstärkt, wenn Tiere aus logistischen und finanziellen Gründen vor allem innerhalb eines zoologischen Verbandes wie der EAZA getauscht werden. Umso wichtiger ist die Optimierung der Zucht, um genetische Varianz und gesunde Tiere zu erhalten. Bei der Planung neuer Paare ist die Prüfung der Stammbäume beider Tiere auf gemeinsame Vorfahren zu empfehlen.

Wenn Küken gehäuft aus Nährstoffmangel sterben, sollte die Ernährung angepasst werden. Lifka (2008) weist für Klunkerkranich-Küken auf einen geringeren Eiweiß- und höheren Grünanteil in der Nahrung im Vergleich zu anderen Kranichküken hin. Außerdem sollte die Aufnahme von Fremdkörpern oder Giftstoffen aufgrund falscher Fütterung durch die Eltern oder ungeeigneter Gehegeausstattung überprüft werden.

Für eine erfolgreiche Brut sollten Paare möglichst jung etabliert werden und abhängig von ihren individuellen Ansprüchen in einer störungsfreien Umgebung gehalten werden. Selbst Gehege mit Besucherexposition ohne Versteckmöglichkeiten und in Nachbarschaft zu anderen Kranichen sind kein Ausschlusskriterium für eine erfolgreiche Zucht. Die Unterbringung sollte an das Verhalten des Kranichpaars adaptiert sein und erfordert häufig Einzelfallentscheidungen. Bei aggressivem Verhalten gegenüber anderen Kranichen sollte ein Sichtschutz oder bei Bedarf eine andere Unterbringung in Betracht gezogen werden. Eine erfolgreiche Zucht mit handaufgezogenen Männchen scheint anhand der Untersuchungen und der Erfahrungen mehrerer Kuratoren sehr unwahrscheinlich zu sein. Die Gültigkeit der Untersuchungen sind aufgrund der kleinen Stichprobe allerdings vorsichtig zu bewerten. Vergesellschaftungen sollten wohl überlegt sein und in keinem Fall zu zusätzlichem Stress oder Gefahr für ein Paar oder deren Küken führen.

Beim globalen Austausch von Klunkerkranichen wird nicht berücksichtigt, welcher der drei Subpopulationen die Individuen entstammen. Sofern in Zukunft die Voraussetzungen für Auswilderungsprojekte gegeben sein sollten, müssten die drei Subpopulationen separat koordiniert werden.

Fazit

Es konnten mehrere Faktoren benannt werden, die maßgeblich für die niedrige Reproduktionsrate von Klunkerkranichen in Haltung verantwortlich sein könnten. Zunächst einmal sollten Handaufzuchten – wenn überhaupt - nur unter strengen Richtlinien und von qualifizierten Tierpflegern durchgeführt werden. Die Unterbringung sollte Haltungsrichtlinien entsprechen, die natürlichen Boden und eine störungsfreie Umgebung vorgeben. Die Identifikation einer geeigneten Gehegeausstattung sowie möglicher Stressoren erfordert häufig eine Einzelfallbetrachtung und somit qualifiziertes und motiviertes Personal. Zu große Ablenkung und Störung durch Tierpfleger, Besucher, und benachbarte oder vergesellschaftete Tiere sollten verhindert werden.

Um die Fruchtbarkeit der Eier im Rahmen einer natürlichen Besamung zu erhöhen, wäre es ratsam, insbesondere Männchen zukünftig nicht mehr zu kupieren. Für bereits kupierte Tiere kann der kontralaterale Flügel beschnitten werden, um die Balance bei der Kopulation zu verbessern. Im Falle von künstlicher Besamung sollte sich an den Legedaten der vorherigen Jahre orientiert werden, da klimatische Einflüsse kaum einen Einfluss zu haben scheinen.

Um die Bedürfnisse dieser anspruchsvollen Vogelart besser zu verstehen und eine artgerechte Haltung zu gewährleisten, wäre eine detailliertere Untersuchung der Fütterung sowie der Gehegebeschaffenheit sinnvoll. Besonders in Einrichtungen, die keine Kranichpellets verfüttern, sollte eine ausreichende Nährstoffversorgung sichergestellt werden.

Für zukünftige Untersuchungen könnte es sinnvoll sein, neben der Störung durch Tierpfleger, Besucher und andere Kraniche auch die Ausrichtung des Geheges sowie die Anzahl der Gehegeseiten zu erfassen, an denen die Tiere Störungen ausgesetzt sind. Dies würde eine fundiertere Bewertung ermöglichen, ob ihnen ausreichende Rückzugsmöglichkeiten im Gehege zur Verfügung stehen.

Bezüglich einer möglichen Fehlprägungen wären zudem Untersuchungen interessant, ob eine frühzeitige visuelle und akustische Sozialisierung mit Artgenossen dieser entgegenwirkt oder warum ein privater Züchter auch mit Handaufzuchten zuverlässig brütende Tiere erhielt.

Danksagung

Ich möchte mich vielmals bei meinem Hauptbetreuer Prof. Dr. Thomas Ziegler bedanken, der sich die Zeit genommen hat, diese Bachelorarbeit zu betreuen und zu korrigieren. Großer Dank

gilt auch meinem Fachbetreuer Bernd Marcordes, der mir mit viel Fachwissen und hilfreichen Anregungen zur Seite stand, etliche Kontakte weltweit etabliert hat und mich auf diese interessante Vogelspezies aufmerksam gemacht hat.

Ich möchte PD Dr. Benjamin Altenhein danken, der seine Zeit investiert hat, um meine Arbeit als Zweitgutachter zu lesen und zu bewerten. Auch meinem Mentor Prof. Dr. Reinhard Predel danke ich für seine Betreuung und Zeit.

Frederick Beall bin ich sehr verbunden für das Engagement und die Unterstützung, mir bei der Kontaktaufnahme zu verschiedenen AZA-Institutionen und regionalen Zuchtbuchführern in China und Südafrika zu helfen. Dank der Unterstützung von Zhang Jing konnte ich Daten von zumindest zwei chinesischen Zoos in meine Analysen mit aufnehmen.

Ich möchte mich bei allen Tierpflegern, Kuratoren, Zoodirektoren, privaten Züchtern und Vogelschützern bedanken, dass sie sich die Zeit genommen haben, sich mit mir über Klunkerkraniche auszutauschen und so zu den Ergebnissen dieser Arbeit beigetragen haben.

Besonderer Dank gilt meiner Familie, meinen Freunden und meinem Partner, die mir mit Ratschlägen und Unterstützung das Schreiben dieser Arbeit erleichtert haben.

Abstract

Due to increasing hydrological interventions and human disturbance, as well as scrub encroachment in wetlands, suitable habitats for the African Wattled Crane (*Bugeranus carunculatus*) are becoming increasingly scarce. To ensure the survival of this endangered bird species, these animals are bred worldwide in human care. As Wattled Cranes have the lowest reproductive rate of all cranes and are particularly difficult to reproduce in captivity, the aim of this study was to identify potential causes for the poor breeding success. To this end, a questionnaire was used to record the husbandry and breeding conditions of the entire ex situ population worldwide and to analyze correlations between those conditions and reproductive success.

Ultimately, data from 130 individuals were included in the dataset, 70 of whom were kept in pairs. The enclosure size had no influence on either aggressiveness or reproductive behavior. A clear effect of the presence of water in the enclosure on welfare and breeding success could not be demonstrated. Hand-reared animals, male animals and animals exposed to visitors were significantly more aggressive. Harmonious mating behavior was not observed only if the animals were mated at 27 years of age or older. Harmonious pair behavior did not correlate with the length of the partnership.

Sexually mature females only laid eggs when they were in pairs or in the vicinity of other cranes. Females that experienced aggressive behavior within the pair were significantly more likely not to lay eggs. Harmonious pair behavior and no aggression within the pair were absolute requirements for fertilized eggs. The assumption that hand-rearing has a negative effect on reproductive success was confirmed in male animals. These produced significantly fewer fertilized eggs and there was no evidence of offspring at all. The hypothesis that flight-capable males produced more fertilized eggs than pinioned or clipped males could not be confirmed. However, it became clear that pinioned males over the age of 20 produced fewer fertilized eggs.

Increasing age had a positive influence on egg care.

It can be concluded from the results that hand-rearing should be avoided, especially for male Wattled Cranes, in the interests of animal welfare, reproductive success and the safety of keepers. Costumed rearing under strict guidelines and early socialization with conspecifics can counteract imprinting on humans.

Re-mating is advisable if there is no pair-bonding behavior, if a pair is aggressive towards each other, or if one of the partners is imprinted on humans. Pinioning is not advisable, espe-

cially for males, as this irreversible procedure also shortens the natural reproductive phase and artificial insemination in Wattled Cranes is a demanding method that can involve significant stress for the animals and high personnel expenditure.

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Anhang

Tab. 5: Institutionen der 130 untersuchten Klunkerkraniche mit Geschlechterverhältnis.
Tab. 5: Institutions of the 130 examined wattled cranes with gender ratio.

Kontinent	Land	Institutionen	♂	♀	?
Afrika	Südafrika	Johannesburg Zoo	3	7	0
		Johannesburg Zoo, Breeding Farm	14	15	1
Asien	Singapur	Singapore Zoo (Mandai Wildlife Reserve)	1	1	0
	China	Dalian Forest Zoo	1	1	2
		Beijing Zoo	1	2	0
Europa	Slowakei	National Zoological Garden Bojnice	1	1	0
	Deutschland	Tierpark Berlin	1	1	0
		Weltvogelpark Walsrode	1	1	0
		Kölner Zoo	1	2	0
		Moonen, Wisbroek	1	1	0
	Tschechien	Prague Zoo	1	2	0
		Zoo Zlín	5	3	0
		Dvůr Králové Zoo	1	1	0
	England	Paignton Zoo Environmental Park	1	1	0
		Whipsnade Zoo	2	5	0
	Spanien	Oasis Wildlife Fuerteventura	0	1	0
	Frankreich	Parc des Oiseaux - Dombes	0	1	0
		Zoo Parc de Beauval	1	1	0
Nordamerika	USA	Albuquerque Biological Park	1	1	0
		North Carolina Zoo	1	0	0
		International Crane Foundation	2	3	0
		Dallas Zoo	1	1	0
		Fort Worth Zoological Park	1	1	0
		Fossil Rim Wildlife Center	1	3	0
		Franklin Park Zoo New England	1	2	0
		Fort Wayne Children's Zoo	1	1	0
		Greenbay NEW Zoo	1	1	0
		Jacksonville Zoo and Gardens	1	1	0
		Louisville Zoological Garden	1	1	0
		ZooTampa at Lowry Park	1	0	0
		Oklahoma City Zoological Park	1	0	0
		San Diego Zoo Safari Park	2	1	0
		White Oak Conservation Center, Yulee	4	5	0
		Atlanta Zoo	1	1	0
	Kanada	Toronto Zoo	1	0	0
Summe			**58**	**69**	**3**

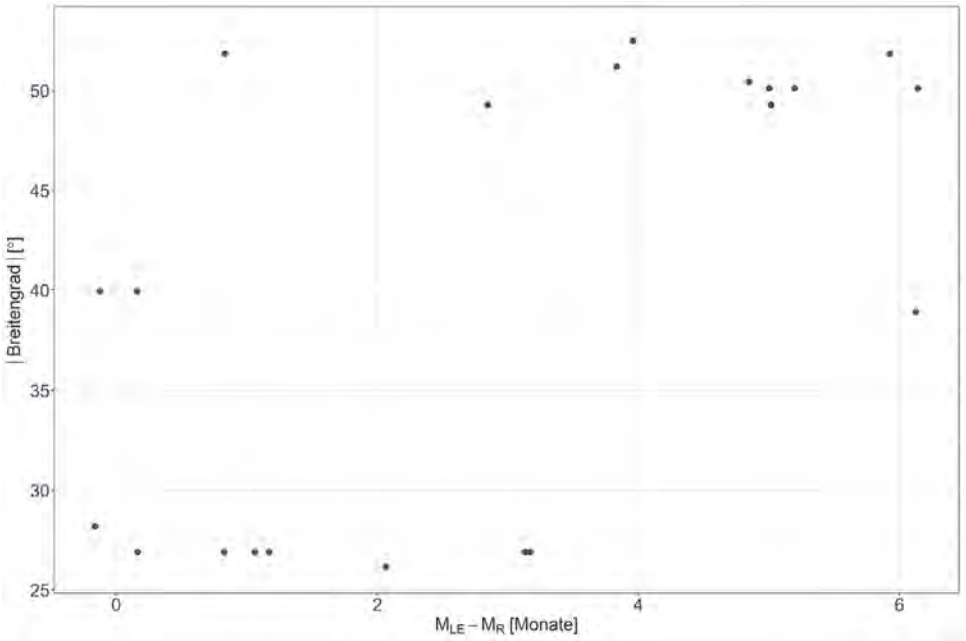

Abb. 5: Streudiagramm der Differenz des Monats der letzten Eiablage (MLE) zum Monat mit der niedrigsten Tageslänge (MR) auf der x-Achse und dem Betrag des Breitengrads der Institution auf der y-Achse. Legedaten der Weibchen aus AZA-Institutionen wurden hier nicht berücksichtigt, p-Wert <0,05, ρ = 0,5

Fig. 5: Scatterplot of the difference between the month of the last oviposition (MLO) and the month with the lowest day length (MLD) on the x-axis and the amount of latitude of the institution on the y-axis. The laying dates of females from AZA institutions were not included here, p-value <0.05, ρ = 0.5

DER ZOOLOGISCHE GARTEN
THE ZOOLOGICAL GARDEN

doi:10.53188/zg0043 Zool. Garten N.F. 93 (2025) 101-122

Initial results on the individual identification of *Telmatobius culeus* (Garman, 1876) using photo documentation

Erste Ergebnisse zur individuellen Identifizierung von *Telmatobius culeus* (Garman, 1876) anhand von Fotodokumentation

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Abstract

This article describes the option of identifying individual frogs of the species *Telmatobius culeus* by taking photos of the individuals. Individual marking is necessary to ensure the exchange of animals between owners and across national borders. The article explains that photo documentation can be a practical and non-invasive method of individual recognition during the first eight and a half years of life. It provides further tips for taking usable photos of frogs, and describes distinctive, recurring spot patterns and skin anomalies. The article closes with a discussion about the changes in the spots and patterns as well as the increasing size of spots that occur with age. Finally, the article provides a note on how to distinguish sexually mature males and females.

Keywords: *Telmatobius culeus*, water frogs, Titicaca giant frog, non-invasive individual identification, conservation, body size

Introduction

The Titicaca giant frog *Telmatobius culeus* (Garman, 1876) is a charismatic amphibian species belonging to the family of Andean whistling frogs or water frogs (Telmatobiidae) Fitzinger, 1843 (see Frost, 2024) and is endemic to Lake Titicaca and its tributaries (IUCN SSC Am-

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phibian Specialist Group, 2020). According to Frost (2024), the genus *Telmatobius* Wiegmann, 1834 comprises 60 species, some of which are endangered or critically endangered. Most of these species are purely aquatic and/or semi-aquatic and inhabit lakes, rivers, wetlands, swamps and similar habitats in the Andean highlands (Ecuador to Chile and Argentina) (Barrionuevo, 2017). Very few species are terrestrial (summary in Honigs et al., 2026 submitted). However, all water frogs have in common that they are under severe pressure due to habitat loss caused by pollution and environmental change, mining, infectious diseases (especially *Batrachochytrium dendrobatidis*), collection by humans and climate change (e.g. de la Riva, 2005; Merino-Viteri et al., 2005; Angulo, 2008a, b; Catenazzi et al., 2010; de la Riva & Reichle, 2014; Zevallos et al., 2016; Cambacho-Badani et al., 2020; Salica et al., 2023; Yao et al., 2023; Swift, 2025).

Telmatobius culeus is listed as endangered in the Red List of the International Union for Conservation of Nature (IUCN) (IUCN SSC Amphibian Specialist Group, 2020) and the population trend is in sharp decline (de la Riva & Reichle, 2014; Ramos Rodrigo et al., 2019). Since January 2017, *T. culeus* has been specially protected under Germany's Federal Nature Conservation Act (BNatSchG) and has enjoyed maximum protection since February of the same year. This species is listed in Annex A of EU Regulation 2023/0966 [EC] and in Annex I of the Washington Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Germany's Federal Agency for Nature Conservation, 2025). In Peru, it is illegal to catch the Titicaca giant frog in the wild, and in Bolivia, catching and trading have also been prohibited since 2016. Since then, trading has also been subject to CITES.

For over 20 years, efforts have been made to promote the keeping and breeding of this species of water frog and to accompany ex situ efforts with a sustainable strategy for environmental education, promoting ethno-folkloric values and encouraging people to control pollution of the lake (Fontúrbel & Richard, 2004). In 2010, a workshop was held to determine how *T. culeus* could be saved from extinction (Reading et al., 2011): the involvement and awareness of the population, conservation breeding, the formation of meaningful partnerships, research and the establishment of protected areas are crucial for success. As a result of the workshop findings, Peruvian politicians became aware of the problem and highlighted the uniqueness of the species. Bolivia and Peru subsequently initiated a joint action plan to protect this amphibian species (Quispe et al., 2023).

In 2017, Denver Zoo became the first zoo in the United States to successfully breed this species outside its native range (Peru and Bolivia) (Weaver, 2017). In 2019, 150 two-year-old frogs from this breeding programme were sent to eleven zoological institutions in Europe (Honigs et al., 2021a, b), including the Aquazoo Löbbecke Museum (hereinafter referred to as Aquazoo) in Düsseldorf (Germany). Breeding this species is easy, so animals could be passed on to other zoological institutions and Citizen Conservation. This approach and the integration of ex situ breeding into conservation and breeding efforts for *T. culeus* are consistent with the One Plan Approach (Byers et al., 2013). Since the breeding of this endangered amphibian species is required for its conservation by the Action Plan for the Conservation of *T. culeus* (Reading et al., 2011; Muñoz, 2013), it is necessary to transport animals and exchange them among the institutions and participants in the breeding programme. Therefore, it is important to develop a tamper-proof method for identifying individual animals. For many animal species, transponder tagging is required by law, but the animals must have reached a minimum body weight of 200 g.

Titicaca giant frogs can reach a body weight of up to 250 g (Hutchison et al., 1976), which takes them quite a while. In our experience, amphibians often lose transponders via various unknown ways, that is why this marking method is not the best choice. In addition, implanting a transponder is costly, as are many other invasive methods of identification. Marking should be as painless and stress-free for the animal as possible, ideally non-invasive and inexpensive. One such method is photo documentation, which has already been used successfully with many an-

imal species of various classes and genera. This method takes advantage of the naturally occurring and distinctive body patterns and characteristics of the animals, such as spots, dots, scales and/or growth lines. However, for the photos to be useful, there must be sufficient variability in the body markings and they must be stable, ideally over many years or throughout the entire lifespan, and a consistently comparable photography method must be used.

For numerous species of tortoises, regular photo documentation against a black-and-white checkered background (Bender, 2001) is an established practice recognised by the authorities. This non-invasive identification method has also proven successful for some snake species (Bender, 2001) and lizards such as *Cnemaspis psychedelica* Grismer, Ngo & Grismer, 2010 (Gewiss et al., 2021), *Lygodactylus williamsi* Loveridge, 1952 (Röll, 2018) and *Intellagama leuseurii* (Gray, 1831) (Gardiner et al., 2014). It is also found in some amphibian species, such as *Leptodactylus fallax* Müller, 1926 (Jameson et al., 2019), *Ceratophrys stolzmanni* Steindachner, 1882 (Bardier et al., 2021), *Bombina variegata* (Linnaeus, 1758) (Plăiaşu et al., 2005), numerous newts such as *Calotriton asper* (Dugès, 1852) (Dalibard et al., 2021), *Triturus cristatus* (Laurenti, 1768) (Matthe et al., 2008), *Neurergus kaiseri* Schmidt, 1952 (Vaissi et al., 2018) and salamanders of the genus *Salamandra* Garsault, 1764 (Bogaerts et al., 2021; Speybroeck & Steenhoudt, 2017). This photo documentation can be simplified and optimised by using appropriate software such as Wild-ID (Bolger et al., 2012), APHIS or Automated PHoto-Identification Suite (Moya et al., 2015).

The basic colouration of *T. culeus* is variable ranging from olive green to dark green, grey and brown tones with light yellow, orange, grey-brown to black spots and/or dots (e.g. Garman, 1876) on the dorsal body surfaces and extremities (Fig. 1a). The basic colouring already shows slight marbling. The frog's bellyside is spotless, light beige to white, more rarely grey in colour (De la Riva, 2005) (Fig. 1b).

This study documents the distinctive and individually unique spots, patterns and/or combinations thereof on the frogs and examines the period over which these natural markings remain unchanged. The possible individual recognition of the animals is being tested. In addition, an easy-to-use and inexpensive method of photo documentation was developed so that both private owners without photography skills and experts experienced in photo documentation can use the photo method.

Materials and Methods

Telmatobius culeus has been kept at the Aquazoo since 2019 and bred since October 2020 (Honigs et al., 2021a, b). Immediately after their arrival from Chester Zoo (UK), the eight frogs were photographed. The frogs reproduced excellently and 31 frogs from the offspring were photographed regularly every six months (38 animals in total). Another 29 frogs were photographed after their metamorphosis but were passed on to other zoos or institutions.

Both a digital SLR camera (Sony DSC-HX400V, 20.4 megapixels, Exmor R) and a smartphone (Sony Xperia 5 and, from November 2024, Fairphone 5 5G) were used for photography. Photos were taken without flash. The frogs are being kept in four aquariums, as described in detail by Honigs et al. 2021a, b.

To separate the frogs for the photo documentation, a standard fauna box was initially used. However, this proved unsuitable because of its corners, a round, transparent box (originally used for fruit gums, capacity 1,200 ml or 2,000 ml) was subsequently used (Fig. 2). The bottom of the box is lined with laminated, round-cut, standardised black-and-white checkered paper (1 cm x 1 cm checks). The box is filled with aquarium water so that the back of the frog to be photographed is well covered. This not only optimises the photo results but also calms the frog.

Fig. 1: A Titicaca giant frog (*Telmatobius culeus*) in an aquarium at the Aquazoo. Irregularly shaped darker spots are scattered across a slightly marbled lighter background. **B** Light-coloured belly side of a young Titicaca giant frog. All photos: Picture archive Aquazoo Löbbecke Museum

Abb. 1: A Titicaca-Riesenfrosch (*Telmatobius culeus*) in einem Aquarium im Aquazoo. Auf leicht marmorierten helleren Grund sind unregelmäßig verschieden geformte dunklere Flecken verteilt. **B** Helle Bauchseite eines jungen Titicaca-Riesenfrosches. Alle Fotos: Bildarchiv Aquazoo Löbbecke Museum

Fig. 2: Transparent round box for photographing the frogs. Laminated graph paper is placed on the bottom and the box is filled with aquarium water.
Abb. 2: Transparente runde Box zum Fotografieren der Frösche. Am Boden liegt laminiertes Karopapier und die Box ist mit dem Aquarienwasser gefüllt.

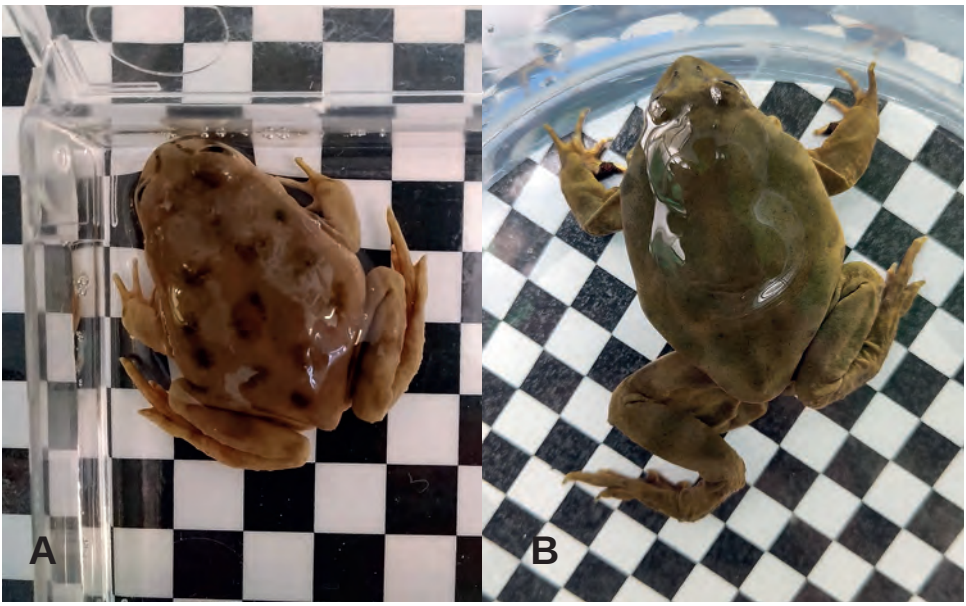

Fig. 3: A A frog was photographed sitting in a box with very little water. The numerous reflections interfere with the image. **B** A frog is not sufficiently covered with water and pushes itself up. This causes annoying reflections.

Abb. 3: A Ein Frosch wurde mit sehr wenig Wasser in einer Box fotografiert. Die zahlreichen Spiegelungen stören das Bild. **B** Ein Frosch ist nicht ausreichend mit Wasser bedeckt und drückt sich hoch. So entstehen störende Reflektionen.

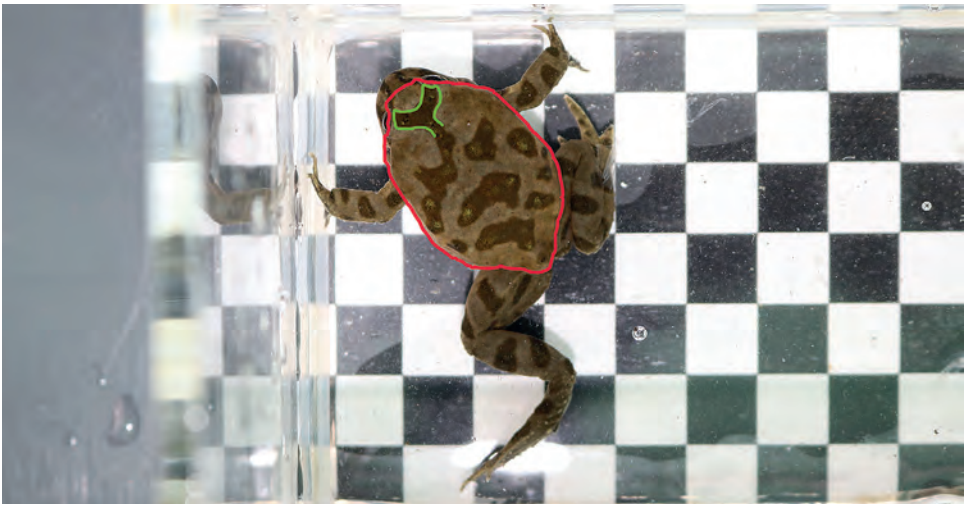

Fig. 4: The area considered for photo documentation is marked (in red). In this animal, it is also easy to see that the eye band transitions into a „Y-shape“ (in green).

Abb. 4: Der Bereich, der für die Fotodokumentation betrachtet wurde, ist markiert (in rot). Bei diesem Tier ist auch gut zu erkennen, dass das Augenband in eine „Y-Form“ übergeht (in grün).

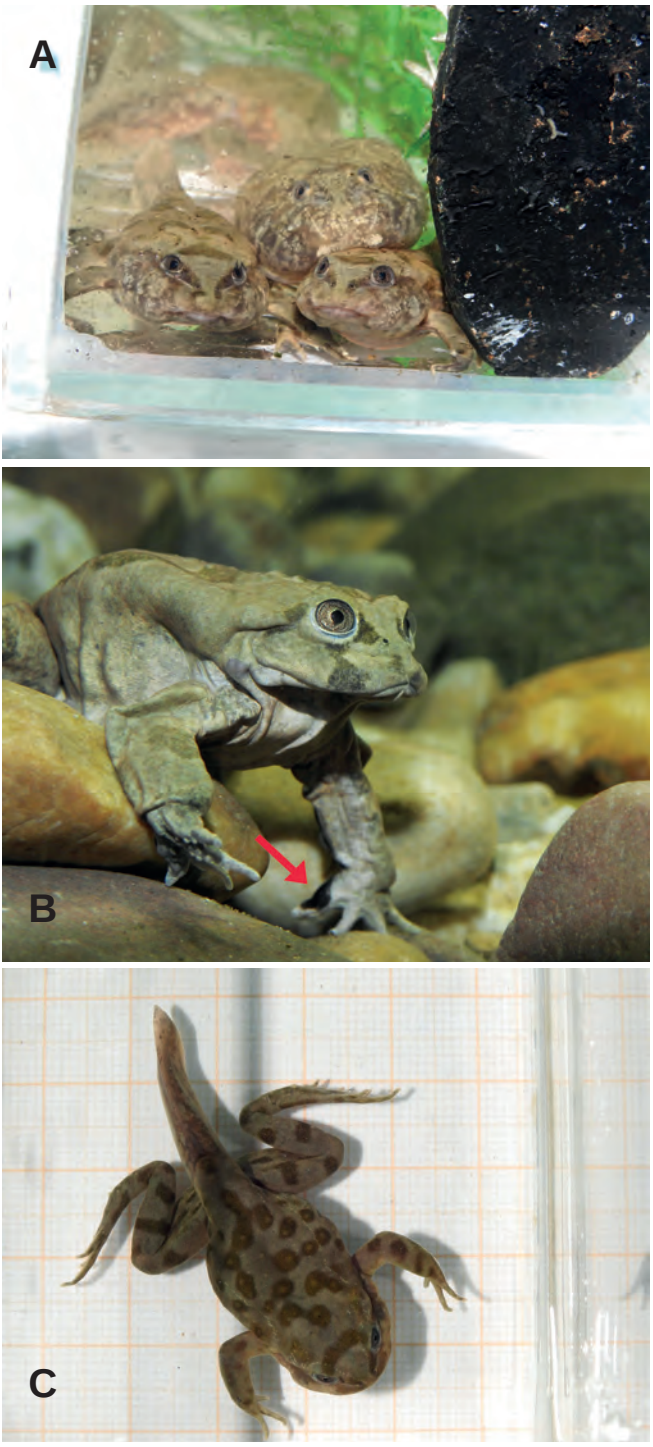

Fig. 5: A The typical facial stripes are clearly visible on the two animals at the bottom of the box in Gosner stage 43. The younger third tadpole still has the marbled pattern typical of younger animals. **B** The facial markings are clearly visible in adult *T. culeus*. The arrow (in red) indicates the triangular, deep black marking on the thumb that all adult males have. **C** In Gosner stage 43, the spots are already well defined and the eye band is visible.

Abb. 5: A Bei den beiden Tieren am Boden der Box im Gosner-Stadium 43 sind die typischen Gesichtsstreifen gut zu sehen. Die jüngere dritte Kaulquappe hat noch das Marmor-Muster das jüngere Tiere zeigen. **B** Beim erwachsenen *T. culeus* sind die Gesichtsmarkierungen gut zu erkennen. Der Pfeil (in rot) kennzeichnet die dreieckige tiefschwarze Markierung am Daumen die alle erwachsenen Männchen aufweisen. **C** Im Gosner-Stadium 43 sind die Flecken bereits gut ausgeprägt und das Augenband ist zu sehen.

Fig. 6: An adult *T. culeus* with larger, relatively uniform dark spots on a lighter background colour.
Abb. 6: Ein erwachsener *T. culeus* mit größeren relativ einheitlich dunklen Flecken auf hellerer Grundfarbe.

If the frog moves, the reflections are minimal. If the frogs are photographed outside the water, their moist skin causes numerous reflections, and the spots are not clearly visible (Fig. 3a and 3b). Reflections on the water caused by incident light can be prevented by using your own upper body. The frogs are always photographed individually in the box from above. Due to the round walls, the frog cannot sit in a corner, which makes taking photographs easier.

Only the individual dorsal markings on the frogs' heads and backs were considered (Fig. 4) to distinguish the animals. The frogs' extremities are usually in different positions, so it would have been too time-consuming and stressful for the animals to bring them into the same body position in order to also use the leg markings for differentiation. The animals' face spots were also not taken into account.

Results

The Titicaca giant frog has a dark stripe running from the inner corner of the eye across the nose to the upper lip. These two stripes become visible as soon as all four limbs are well developed after around 177 days (stage 43 according to Gosner, 1960) (Fig. 5a). Another stripe runs from the lower eye to the upper lip. These four stripes are typical of the species and can be seen on all 38 young frogs and older frogs (Fig. 5b, c). Almost all frogs have an elongated, transverse spot behind each eye, with these spots merging in the centre behind the eyes to form a slightly posteriorly curved

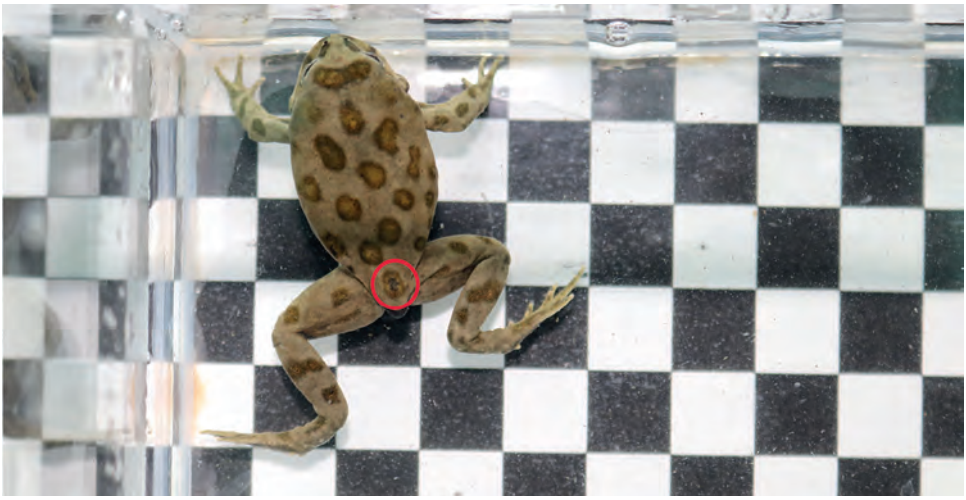

Fig. 7: A young *T. culeus* with spots that are light yellow on the inside. The animal also has a noticeable skin or colour anomaly (circled in red).
Abb. 7: Ein junger *T. culeus* mit Flecken, die innen hell gelb gefärbt sind. Zudem weist das Tier eine auffällige Hautanomalie auf (eingekreist in Rot).

Fig. 8: An adult *T. culeus* with large spots that are lighter on the inside. The animal also has a colour anomaly (circled in red).
Abb. 8: Ein erwachsener *T. culeus* mit großen Flecken die innen heller sind. Zudem hat das Tier eine Farbanomalie (eingekreist in Rot).

Fig. 9: An adult frog with large spots and additional small dark dots.
Abb. 9: Ein erwachsener Frosch mit großen Flecken und zusätzlich kleinen dunklen Punkten.

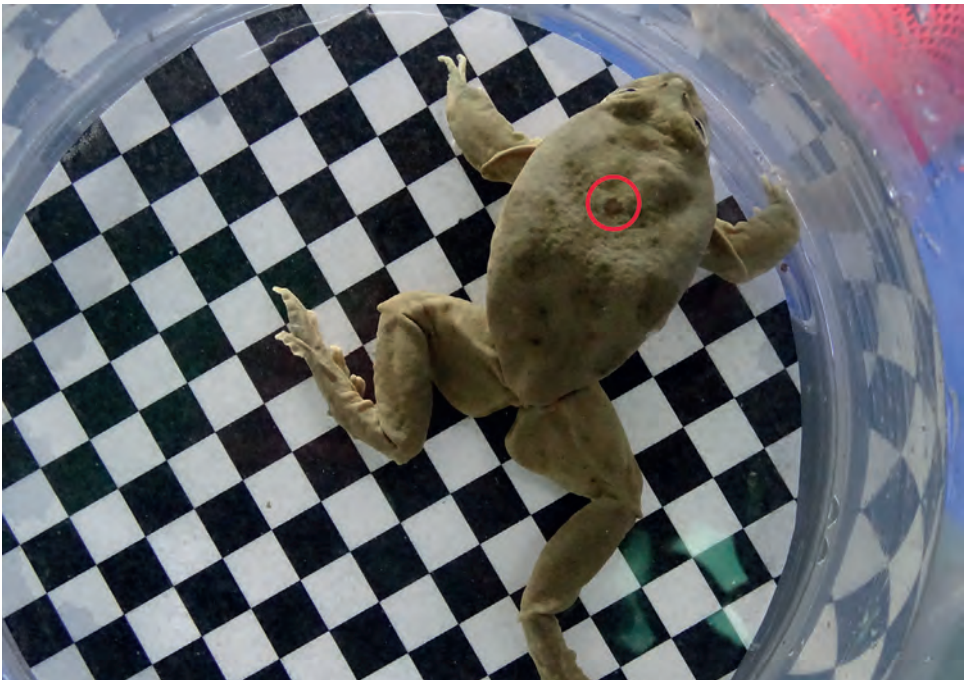

Fig. 10: This frog has a striking dark pigment spot on its back (circled in red).
Abb. 10: Dieser Frosch hat einen auffälligen dunklen Pigmentfleck auf dem Rücken (eingekreist in Rot).

Fig. 11: An adult frog with distinct granulomas spread across its body. The colouring and spots are very pale and blurred. This animal comes from Denver Zoo and had only faint spots from the outset. At the time the photo was taken, it was 101 months old and 6.72 cm tall.
Abb. 11: Ein erwachsener Frosch mit deutlichen Granulomen über den Körper verteilt. Die Färbung sowie die Flecken sind sehr blass und verschwommen. Dieses Tier stammt aus dem Denver Zoo und hatte von Beginn an nur schwach ausgeprägte Flecken. Zum Zeitpunkt der Aufnahme war es 101 Monate alt und 6,72 cm groß.

spot (eye band). The eye band, which also becomes visible after around 177 days (Fig. 5c), can merge posteriorly into a stripe or spot, making it look like an 'Y' (Fig. 4). Larger spots are spread across the back and legs. These large spots (main spots or stains) are usually dark grey-brown and vary in number, size, shape and brightness. However, the main spots are usually uniformly dark in colour and clearly distinguishable from the basic colour of the body (Fig. 6). In some animals, the main spots have a dark outline and are lighter in colour on the inside (Fig. 4, 7 and 8). In addition, small spots, which are more like dots and are usually darker, may appear next to the large main spots. These small spots are spread on the back and legs, between and on the main spots (Fig. 9). Less commonly, individual black pigment spots occur in the frogs at the Aquazoo, which may not have been visible immediately after metamorphosis (Fig. 10). In addition, clearly visible granulomas occur, which can appear as small light spots on the skin and can also occur within a main spot (Fig. 11). A change in skin colour in the form of a spot was observed in one frog and remained visible after it initially appeared (Fig. 7 and 8).

In summary in *T. culeus*, several recurring spot patterns can be identified in different individuals: double horseshoe (Fig. 12), bone (Fig. 13, 14), „Y" (Fig. 4), large and uniformly coloured

Fig. 12: This frog has a double horseshoe-shaped spot on its back that immediately connects to the 'Y-shape'. It also has typical uniformly coloured spots on its back.
Abb. 12: Dieser Frosch zeigt einen Fleck in Form eines doppelten Hufeisens auf dem Rücken der sofort an die „Y-Form" anschließt. Zudem hat er typische einheitlich gefärbte Flecken auf dem Rücken.

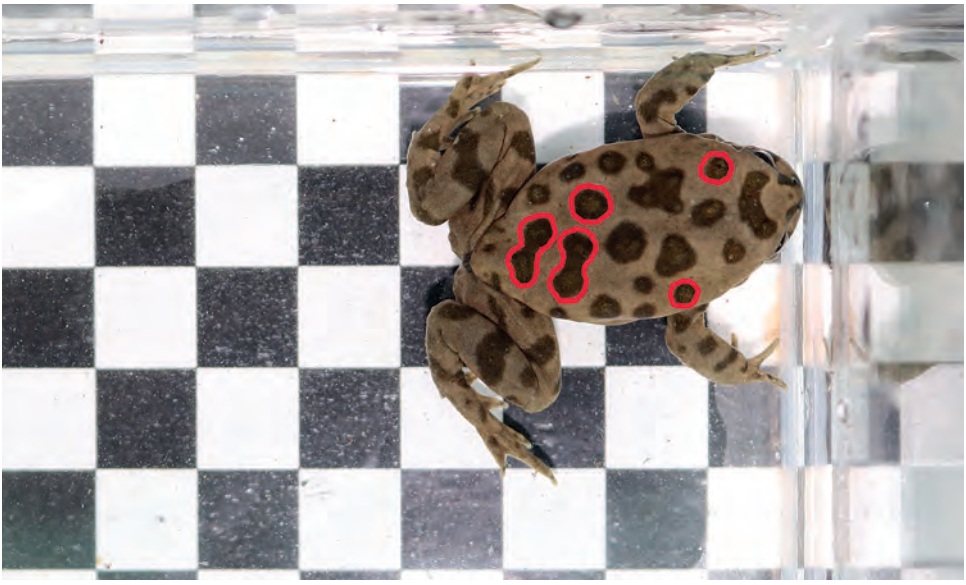

Fig. 13: A young frog with round and bone-shaped spots (each with a border in red).
Abb. 13: Ein junger Frosch mit runden sowie knochenförmigen Flecken (jeweils umrandet in Rot).

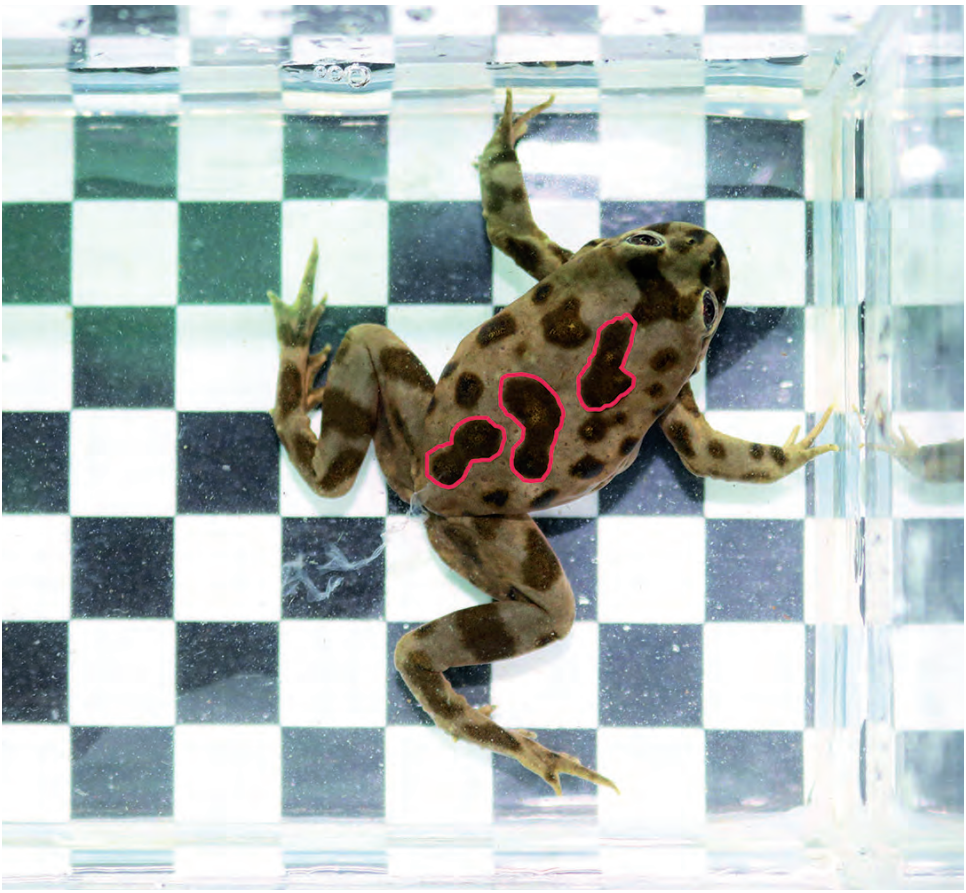

Fig. 14: A young frog with hammer-shaped and bone-shaped spots (each outlined in red).
Abb. 14: Ein junger Frosch mit hammer- sowie knochenförmigen Flecken (jeweils umrandet in Rot).

spots (Fig. 6), light or yellow-filled spots (Fig. 4, 5c, 7, 8), round spots (Fig. 13), Hammer- or club-shaped (Fig. 14) and small spots or dots with intense dark colouring (Fig. 9). Even in tadpoles (from around day 177), distinctive spots can be seen on the animals' backs, which also occur in different individuals. We could not detect any differences in spots, colouring or pattern forms between males and females. However, adult male *T. culeus* have a deep black triangular mark on the inside of their thumb (Fig. 15a-c). This mark is not present in females. The age at which this triangle can be seen cannot yet be described.

The check pattern can also be used to measure the growth of individual frogs per year. The animals bred in the Aquazoo grew continuously by an average of approximately 0.5 cm per half year in the various aquariums. However, this observation only applies to animals that were also bred at the Aquazoo. The animals from Denver (USA) grow more slowly. This observation cannot currently be explained with certainty and could only be related to the breeding conditions (water, temperature, food, etc.) during the first phase of life until metamorphosis. One of the oldest animals at the Aquazoo, which came from Denver Zoo, is currently 7 cm tall.

Since 2019 and 2020, the dorsal spots of most of the frogs regularly photographed at the Aquazoo have been hardly changed until today, so that the individual animals can still be dis-

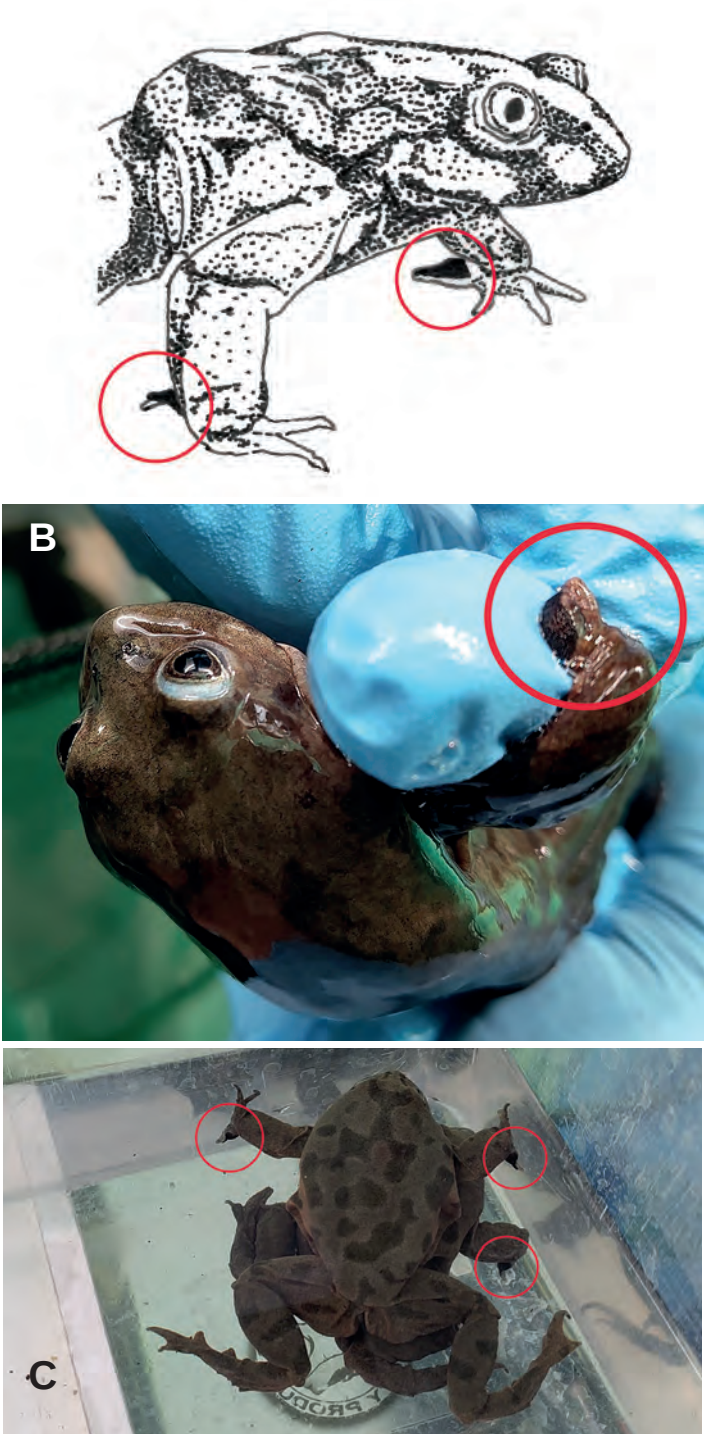

Fig. 15: A The drawing shows an adult male *T. culeus* with the typical deep black triangles on the thumb (circled in red). Drawing: S. Honigs. **B** The thickened, black area on the thumb of this adult male *T. culeus* is clearly visible (circled). **C** Two male *T. culeus* viewed from above. The black markings on the thumbs (circled in red) are clearly visible.

Abb. 15: A Die Zeichnung zeigt einen erwachsenen männlichen *T. culeus* mit den typischen tief schwarzen Dreiecken auf dem Daumen (eingekreist in Rot). Zeichnung: S. Honigs. **B** Die verdickte, schwarze Stelle am Daumen dieses erwachsenen männlichen *T. culeus* ist gut zu erkennen (eingekreist in rot). **C** Zwei *T.-culeus*-Männchen von oben. So sind die schwarzen Markierungen an den Daumen (eingekreist in Rot) gut zu erkennen.

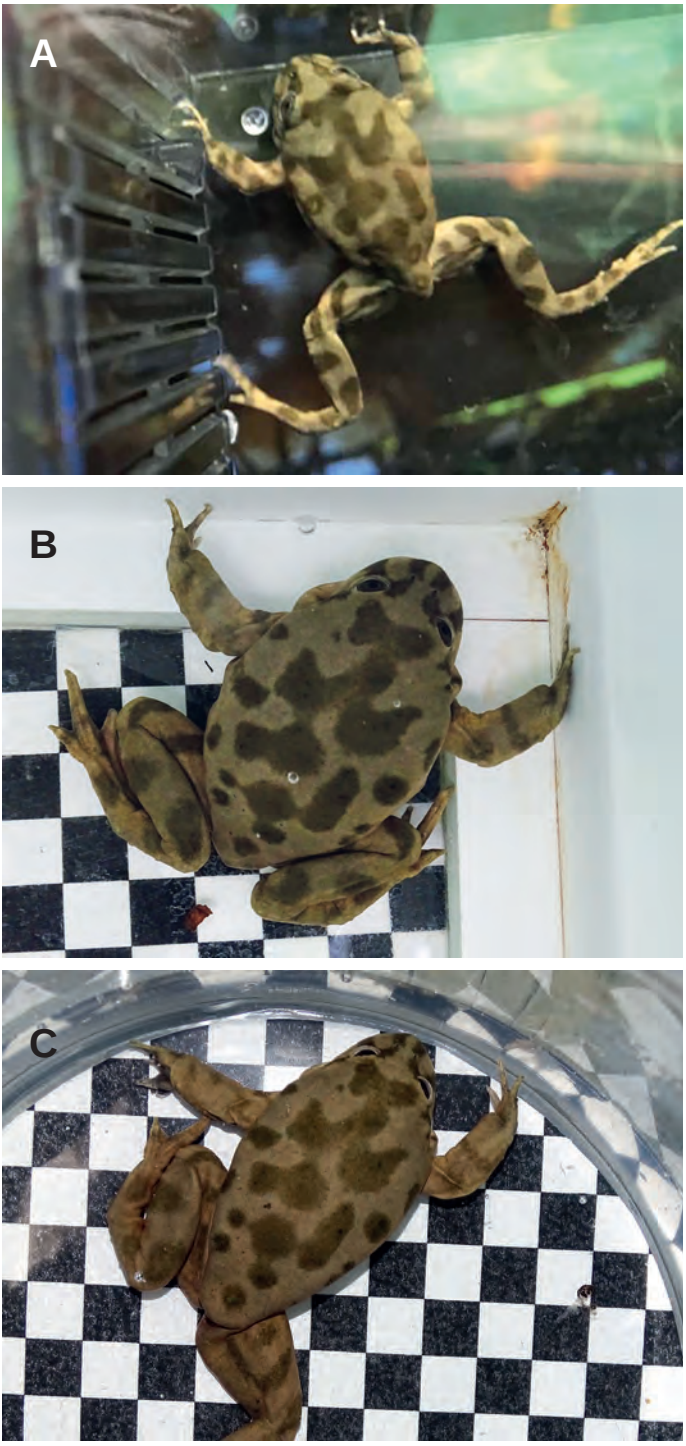

Abb. 16: Spot development in a female Titicaca giant frog number A147, metamorphosis completed in August 2021. **A** Photo from August 2021, 2.9 cm. **B** Photo from December 2023, 5.5 cm. **C** Photo from January 2025, 6.25 cm. The frog is currently 6.5 cm tall (August 2025). The distinctive spots remained unchanged during the first four years of the frog's life after metamorphosis was complete. This is an example where the stains are very clearly visible, even after many years.

Abb. 16: Fleckenentwicklung beim weiblichen Titicaca-Riesenfrosch Nummer A147, Metamorphose beendet im August 2021. **A** Foto vom August 2021, 2,9 cm. **B** Foto vom Dezember 2023, 5,5 cm. **C** Foto vom Januar 2025, 6,25 cm. Aktuell ist der Frosch 6,5 cm groß (August 2025). Die markanten Flecken blieben in den ersten vier Lebensjahren des Frosches nach Abschluss der Metamorphose unverändert. Dies ist ein Beispiel, bei dem die Flecken sehr gut, auch über die Jahre hinweg, zu erkennen sind.

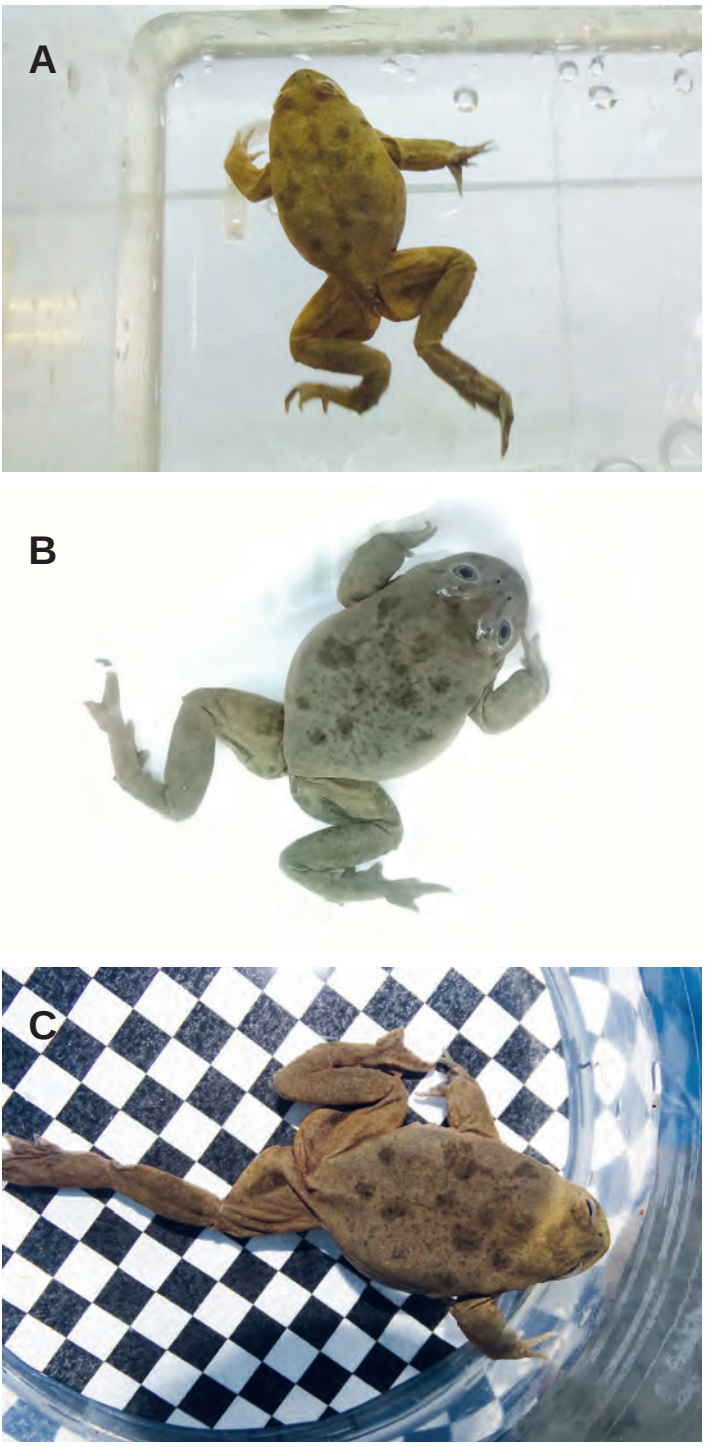

Fig. 17: Spot development in Titicaca giant frog number A108. This female frog came to us from Denver Zoo in May 2019. **A** Photo from May 2019, approx. 5 cm. **B** Photo from July 2022 without measurement, **C** Photo from January 2025, 6.5 cm. Currently (August 2025), the animal is a good 7 cm in size.

Abb. 17: Fleckenentwicklung beim Titicaca-Riesenfrosch Nummer A108. Dieser weibliche Frosch kam aus dem Denver Zoo im Mai 2019 zu uns. **A** Foto vom Mai 2019, etwa 5 cm. **B** Foto vom Juli 2022 ohne Messung, **C** Foto vom Januar 2025, 6,5 cm. Aktuell (August 2025) ist das Tier gut 7 cm groß.

tinguished (compare photo series 16 and 17). There are no differences in the spots and patterns between males and females.

Discussion

Body patterns

Apparently, *T. culeus* lose their 'youth pattern' with age, which transforms into a marbled pattern. When exactly this pattern transformation process begins and ends must be further observed. Only when reliable data is available, more concrete recommendations can be made for the possible use of photo documentation. Until then, it can be stated that photo documentation is a reliable way to identify the animals at least up to the age of eight years.

There are numerous photos of large frogs from Lake Titicaca with strong marbling, so it can be assumed that the spots on young frogs disappear with age and increasing body size and become smaller (cf. images in CITES 2016; Knoll, 2017; Miranda et al., 2019; Muñoz-Saravia et al., 2020; Honigs et al., 2021b; Huisa-Balcon et al., 2022). Upon closer inspection of these marbled frogs, it is noticeable in some cases that the darker spots that were once present still remain as 'shadows' on the skin. In future, it will be necessary to document at what age the clearly defined spots disappear and the small-spotted marbling develops. A photo featured in the IUCN Red List (4/6, Arturo Munoz, IUCN SSC Amphibian Specialist Group, 2020; also in Citizen Conservation, 2025 p. 22, bottom left) shows two frogs swimming in amplexus, with the male resembling animals living in Europe in terms of colouring and markings. However, the clamped supposed female shows the familiar small-scale marbling often seen on photos of the large frogs from Lake Titicaca. The clamped animal is also considerably larger than the clamping animal. This may indicate that the older and larger animals in their natural habitat take on a different pattern over time. It is possible that the strong UV radiation at high altitude is responsible for the fact that *T. culeus* increasingly develops a marbled pattern with many dark spots and small patches as it ages.

Maximum age, sexual maturity and body size at high altitudes

According to current knowledge, Titicaca giant frogs can reach an age of 14 to 20 years in human care (IUCN SSC Amphibian Specialist Group, 2020). Ectothermic animals achieve a longer lifespan and grow more slowly at high altitudes (Zhang & Lu, 2012; Ma et al., 2009). Even in individuals of the same species, such as the native common toad *Bufo bufo* (Linnaeus, 1758), altitude and ambient temperature have an influence on growth rate and body size. Due to their large distribution area and the fact that they colonise different habitats at varying altitudes, it is particularly easy to make intraspecific comparisons under different conditions in the case of common toads. For habitats at higher altitudes and with colder ambient temperatures, common toads grow more slowly than their conspecifics living in lower and warmer habitats (Hemelaar, 1988). Anurans such as *B. bufo* also live longer in cooler habitats than in warmer environments (Hemelaar, 1988). Many amphibian species reach a larger body size at high altitudes than their counterparts in lower-lying habitats (Ashton, 2002). However, this does not apply to all species and habitats around the world. In Tibet, for example, frogs such as *Nanorana parkeri* (Stejneger, 1927) remain smaller when living at high altitudes than in lower-lying habitats (study area between 3,800 and 4,700 metres above sea level) (Ma et al., 2009). According to the authors, animals of this species living in habitats at higher altitude exhibit delayed metamorphosis and sexual maturity as well as longer growth periods. However, they reach a higher average age

than their counterparts at lower altitudes. In tropical regions, on the other hand, many anurans reach sexual maturity relatively early, remain smaller and have a lower life expectancy (Sinsch & Dehling, 2017). This pattern contrasts with that of anurans in temperate zones, which reach sexual maturity later, are larger and live significantly longer.

Given the oxygen-poor and cold habitat at 4 to 14 °C and the associated low metabolic rate, which is the lowest of all anurans (Hutchinson et al., 1976), we assume that *T. culeus* has a long grow period or even grows throughout its entire life and could reach a correspondingly long lifespan of over 20 years. The generation length has already been corrected once in the Red List based on increasing knowledge about the biology of this species and raised from five to 14 years (IUCN SSC Amphibian Specialist Group, 2020). However, to prove or disprove this hypothesis, at least another 11 years of keeping this species in captivity are needed. Titicaca giant frogs reproduce at the age of two years long before reaching their maximum body size of 145 mm (according to Vellard, 1951) or the historically described 50 cm (according to J.-Y. Cousteau in Mantilla Mendosa, 2023). After metamorphosis, anurans grow rapidly for one to two years, after which growth often slows down significantly depending on the species and habitat (Turner, 1960). The growth rate of amphibians decreases after reaching sexual maturity. However, female amphibians need to reach a certain minimum size to lay eggs and usually reach sexual maturity before they are fully grown (Iturra-Cid et al., 2010). Although they continue to grow thereafter, it is never certain whether they will reach the maximum possible body size for their species before they die.

It is unknown how old large specimens of *T. culeus* in Lake Titicaca were when sighted/caught today and in the past. It must be assumed that frogs in the wild today rarely grow as large as they did 100 years ago, as they die prematurely because of numerous external influences. The habitat conditions for frogs in Lake Titicaca used to be much better than they are today. Studies by Sinsch & Aguilar-Puntriano (2021) showed that even in Lake Junín (Peru), frogs, namely the largest aquatic frog *Telmatobius macrostomus*, no longer reach the historically described body size of 30 cm and a weight of 2.8 kg (Fjeldså, 1983). A study using skeletochronology (described in Sinsch, 2015, among others) could help answer the question of the age structure of the *T. culeus* population living in Lake Titicaca. Dead specimens found at the lake or museum specimens would be suitable for examining their skeletons. In the case of *T. macrostomus*, skeletal chronology has shown, among other things, that frogs reach sexual maturity later in their natural habitat than in human care (Sinsch & Aguilar-Puntriano, 2021). According to the authors, the discrepancy is around one year. At extreme altitudes, such as Lake Titicaca (3,809 m above sea level, Hutchinson et al., 1976; TRÓPICO, 2011), various conditions such as UV radiation, air pressure, temperature, dissolved substances in the water, seasonal climatic changes, etc. can have a major influence on the growth of frogs, which are not easy to simulate in human care and are therefore usually omitted. In particular, the ambient temperature has a significant influence on metabolism (Gillooly et al., 2001). Climatic factors such as ambient temperature, UV radiation and humidity have a strong influence on amphibian populations, as they can affect larval growth, sexual maturity, maximum body size and much more (Hemelaar, 1988; Siqueira & Rocha, 2013). Depending on the enclosure conditions, the frogs could exhibit different growth rates, with possible effects on the duration of recognisability of individuals through photo documentation. The younger animals raised at Aquazoo grow 0.5 cm every six months and currently reach a maximum size of 6.5 cm. Animals from Denver Zoo that are three years older are currently about 7 cm in size. This seems to indicate that animals grow more slowly between the ages of five and eight.

Photography is prone to errors, and individual recognition only works if the photos are sharp, of good quality and free of reflections. The more individuals there are to distinguish from one another, the more time-consuming it is to take the photos and evaluate them. Computer-assisted image analysis, which is already used for other species (e.g. Wild-ID, APHIS, AmphIdent),

can be helpful (Matthe et al., 2008; Goedbloed et al., 2017). For the animal's welfare, photo documentation is initially the recommended method of choice. The stress of capture is present in all marking methods, but non-invasive, painless photography only takes a few minutes. We were able to show that the dorsal spot pattern of *T. culeus* is suitable for photo identification of individuals up to an age of eight years. Individual identification by photography has already been successfully applied to another *Telmatobius* species, namely *T. brachydactylus*. Here, the chin and the dorsal body area were identified as high-contrast body parts (Castillo et al., 2024). Photography can be included as part of a comprehensive population monitoring protocol for this species in the future. This should be used by herpetologists and citizen scientists as part of a citizen science project to document population developments. Since the dorsal spot pattern of this species is similar to that of *T. culeus*, we can assume that photo identification can also be carried out effectively by scientists and trained private people in the case of the Titicaca giant frog. For *T. brachydactylus*, only the dorsal head region was considered, but for *T. culeus*, we recommend considering the entire dorsal body region (excluding the extremities) for reliable identification. For *T. macrostomus*, the chin and dorsal head region were photographed in the study by Castillo et al. (2024), but here the spot combinations are too similar, and thus there is too little variability, making the evaluations more difficult. For *T. brachydactylus*, only slight fading of the spots occurred during the study (Castillo et al., 2024).

Conclusion

At least up to the age of eight and a half years, Titicaca giant frogs can be distinguished by the spots on their back. The animals grow minimum until the age of eight, although they can reproduce already from the age of two. The age structure of the animals living in Lake Titicaca would be helpful in comparing the animals' body sizes and patterns with those in human care. Regular photo documentation of the animals kept at the Aquazoo will continue to define, amongst others, the age at which the 'juvenile pattern' changes and to clarify whether the marble pattern of the older animals can also be used for individual identification. Initially, we recommend photographing the animals every six months from above on a standardised checkered pattern as described above. Almost everyone now uses a smartphone, and these devices are ideal for taking photos of the frogs.

Acknowledgements

The authors would like to thank the Office for Environmental Protection and Consumer Protection of the State Capital Düsseldorf (Germany) for its many years of generous financial support for the amphibian breeding and conservation station at the Aquazoo Löbbecke Museum. Thanks go also to Maerte Siemen (Cologne Zoo) for reviewing an earlier version of this manuscript and to Eva Haas for support in translation work. We would also like to thank all our colleagues at the Aquazoo Löbbecke Museum, who have repeatedly supported the project with advice, practical assistance and collegial exchange.

Zusammenfassung

Dieser Artikel befasst sich mit der möglichen individuellen Erkennung von Fröschen der Art *Telmatobius culeus* anhand von Fotos der einzelnen Tiere. Eine individuelle Kennzeich-

nung ist erforderlich, um den Austausch von Tieren zwischen Besitzern und über Landesgrenzen hinweg zu gewährleisten. Der vorliegende Artikel zeigt auf, dass die Fotodokumentation eine praktische und nicht-invasive Methode zur individuellen Erkennung während der ersten 8,5 Lebensjahre sein kann. Es werden Tipps für eine einfache Fotografie von Fröschen gegeben und charakteristische, wiederkehrende Fleckenmuster und Hautanomalien beschrieben. Die Veränderungen der Flecken und Muster mit zunehmendem Alter und der Größe der Tiere werden diskutiert. Ein Hinweis zur Unterscheidung zwischen geschlechtsreifen Männchen und Weibchen wird gegeben. Ferner scheinen die Tiere auch nach Erreichen der Geschlechtsreife weiterhin zu wachsen.

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DER ZOOLOGISCHE GARTEN
THE ZOOLOGICAL GARDEN

doi:10.53188/zg0044 Zool. Garten N.F. 93 (2025) 123-135

Finding Balance: The rise of zoo animal nutrition

Das Gleichgewicht finden: Der Aufstieg der Tierernährung in Zoos

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Abstract

Zoo animal nutrition, as an applied scientific field, is roughly a century old and has seen significant development and impact in changing feeding practices within modern zoos. Whilst the history of zoo animal nutrition has been documented within the profession, how and why zoo feeding and zoo nutrition has changed has generally not be addressed. This paper adds to this existing literature by providing an historicised sociological interpretation of the development of zoo animal nutrition. Zoo animal nutrition as an applied science has developed at quite a pace since its establishments in the early 20th century. Modern zoo feeding practices have changed with the knowledge created by zoo animal nutrition but also in line with the zoos' evolution from statements of imperial power to spaces of scientific curiosity and entertainment to conservation-oriented institutions focused on planetary health. The origins of scientifically informed zoo nutrition can be traced back to the work of the Penrose Research Laboratory (est. 1901) at Philadelphia Zoo. Investigations into causes of death of the zoos collection led by Dr Herbert Fox enabled research by Dr Ellen Corson-White who linked dietary deficiencies to disease and mortality. These findings were further developed by Dr Herbert Ratcliffe who developed "zoo cake" – the first manufactured complete feed for zoo animals – which aimed to standardise and optimise nutrition while reducing disease. The adoption of manufactured diets sparked a philosophical and practical debate, exemplified by the 1966 International Zoo Yearbook exchange between Ratcliffe and Heini Hediger. Ratcliffe prioritised internal health metrics and efficiency, whereas Hediger warned against behavioural impoverishment and "domestication" through artificial feeding. This clash crystallised the epistemic divide between pathological science and ethological observation, a tension that persisted through the century. During the final few decades of the 20th century, zoo animal nutrition entered a period which can be characterised as a "nutritional turn." This period would see attempts to institutionalise the field through conferences such as the Dr Scholl Nutrition Conferences and the 1999 European Zoo Nutrition Research Group meeting. Zoo feeding increasingly integrated behavioural ecology with nutritional science. The period also saw the emer-

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gence of the zoo nutritionist as an employed position in zoos, although uptake across institutions remained limited. Present-day zoo nutrition reflects a negotiated balance between evidence-based nutrient provision and the promotion of natural feeding behaviours developed during the nutritional turn with more traditional approaches. The contemporary zoo nutritionists are "ark diplomats", highlighting their mediating role between science, husbandry practice, institutional priorities, and animal welfare. While the field has advanced markedly since its early 20th-century roots, institutional integration remains incomplete. Greater recognition and empowerment of zoo nutrition expertise is essential to meet the intertwined challenges of animal welfare, biodiversity conservation, and planetary health in the 21st century.

Introduction

The modern 21st century zoo is an institution that in many ways is almost unrecognisable from the formative years of modern zoos of the 19th and early 20th centuries.[1] Even those who have been founded since the Hagenbeck revolution of the early 20th century (Rothfels, 2002) have changed greatly in ethos, design, animal welfare, management and organisation of their living collections. The four pillars of the modern zoo: conservation, education, research and recreation, are themselves being reviewed and addressed by the zoo community. Spooner et al. (2023 and 2025), have noted that the four pillars no longer accurately reflect the 'multifaceted roles that zoos/aquariums fulfil in the 21st century' or the connections zoos have with society and their value (Spooner et al., 2023, 2025). In the last 100 years, zoos have progressed from sites of imperial power statements to scientific curiosity mixed with entertainment, and more recently to locations of conservation. A ubiquitous element of the zoo that has changed alongside the outward mission statement, and that can be argued as a marker of change in zoos, is zoo feeding - once an unhindered pastime of zoo visitors alongside the zoos' everyday activities from the princely menageries of the 18th century through to the pre-war zoos of the 20th century. However, the founding of zoo animal nutrition as an applied science at the Penrose Research Laboratory at Philadelphia Zoo in the early 20th century caused a shift in the practice of zoo feeding.

The scientific development on zoo animal nutrition birthed debate, specialists groups, agreement, disagreement, changes in practices and resistance. It pitted great zoo minds against one another, zoo scientists against zookeepers and brought them together. Changes in zoo nutrition and feeding practices can also highlight the differences in approaches across the global zoo industry both historically and today.

This paper provides a historicised sociological interpretation of these changes, drawn primarily from scientific articles and conference presentations throughout the 20th century. The article argues that the zoo animal nutrition developed from a route to solving diseases and death through nutritional deficiencies but that it has evolved over last 100 years to balance the differing perspectives of zoo professionals leading to a best-practice approach of balance between nutritional requirements with natural animal behaviours, ideally promoting an animal-centric approach to care for zoo animals in captivity. The article concludes with a characterisation of zoo nutritionists and zoo nutrition in the 21st century as one of diplomacy and careful attempts to continue to change practices of care through feeding via evidence-based scientific knowledge combined with the *art* of feeding a diverse range of captive exotic animals.

[1]The modern zoo era arguably commenced with the opening of Tiergarten Schöbrunn, Vienna to the public in 1765; this was followed by Zoo Jardin des Plantes in Paris in 1794, and London Zoo in 1828 – widely considered to be the first scientific zoo (Fisher, 1967; Marvin and Mullan, 1987; Baratay & Hardouin-Fugier, 2002).

Ratcliffe's Zoo Cake

Zoo animal nutrition, as an applied science, has been a key element to the care and management of animal welfare and health in zoos for the last century (Crissey, 2001; Fens and Clauss, 2024). Whilst experimentation and research into zoo feeding can be traced back to the late 19th century with work like that of John Bland-Sutton (Woods, 2018), modern zoo animal nutrition traces its roots back to the practices developed at the Penrose Research Laboratory at Philadelphia Zoo in the early 20th century where the aim was to combat diseases and nutritional deficiencies. The approach of nutritional science changed practices of care in zoo feeding by adding the science to the art of feeding diverse and complicated zoo collections (Dierenfeld, 1996).

Whilst zoo feeding in the 21st century modern zoo is not always a universal endeavour, the innovative edge of zoo feeding, mostly in scientific and conservation focused zoos, began through the work of the Penrose Research Laboratory, established in 1901 at Philadelphia Zoo. The impetuous was to gather knowledge for its own sake but it produced, according to Charles B. Penrose (the American surgeon and zoologist), significant practical value that led to improvements in hygiene and the elimination of some diseases in the zoo (Fox, 1923). Penrose, in his forward to *Disease in Captive Wild Mammals and Birds* (1923), notes that in the late 19th century to early 20th century (prior to the laboratory) the autopsies of animal deaths at Philadelphia only took place when an animal of significance had died.

This changed with the opening of the research laboratory, led by Dr Herbert Fox and his team of pathologists. In the early 20th century, the laboratory performed nearly 6,000 autopsies over two decades. Ellen Corson-White, part of this team of pathologists, is significant to the story of zoo animal nutrition as her work focused on dietary and nutrition issues – of which acute gastroenteritis was the most common disease – as discovered through the animal autopsies (Corson-White, 1923, p. 423). For example, in the Diseases in Captive Wild Mammals and Birds publication, Corson-White's chapter on 'The relations of diet to disease' (1923, 415-461) covers the need for a proper diet in zoo animals and how zoo animals must obtain maximum development, maintain a normal weight curve, show minimum susceptibility to disease, live out a full term of life, breed normally, and rear healthy offspring, capable of an independent life after weaning, and must fulfil the calorific needs of the body (Corson-White, 1923).

Furthermore, the diet must take into account the physical and morphological demands of the animals' gastrointestinal tract and the chemical content must be in a useable form inside the animal body (Corson-White, 1923). The awareness of the needs of zoo animals and efforts needed to prevent nutritional deficiencies and diseases are clear outcomes from the laboratories work over the previous two decades. It was not articulated how Philadelphia Zoo made changes to its feeding practices as a result of the findings yet. This would come later in the 1930s, through Dr Herbert Ratcliffe – another pathologist at the laboratory – and his promotion of 'zoo cake'.

Zoo cake was initially designed by Corson-White to combat bone disease in primates at the zoo (Crissey, 2001). It was developed and extended by Ratcliffe in the 1930s and used as a component of the diets for most of the zoos collection. Zoo cake was designed by Corson-White's initial primate recipe and from the results of the twenty-year period of autopsies at Philadelphia where evidence or indications of malnutrition were identified. Ratcliffe's diets are separated into three feeding typologies, omnivorous, herbivorous, and carnivorous. At each point of the introduction of the new diet, the previous diets are noted and instructions for preparing the manufactured feeds and schedule for feeding are provided (Ratcliffe, 1940). Justification for the diet changes are not specifically mentioned although it is clear the main concern was to reduce disease and improve the health of the collection. This is reinforced by the markers for success through positive changes in death rates, birth rates and infant development.

The knowledge and success of these diets were co-produced by dead and living zoo animals, although they themselves were viewed only as objects and their lived experiences are only visible through statistics and records of deaths, births, and disease. Designing these diets was additionally aided by comparison with the known requirements from wild animal diets and closely related species or as Ratcliffe put it, "*whether man or domesticated animal*" (Ratcliffe, 1940, p. 463).

For the omnivorous animals, which included "subhuman primates", the manufactured feed consisted of ground boiled horsemeat, rolled oats, whole wheat meal, soybean oil meal, peanut oil meal, yellow corn meal, dry buttermilk, brewer's yeast (dry), alfalfa leaf meal, oyster shell flour, iodized salt, and cod-liver oil concentrate. The composition was made up of 25% protein, 5% fat, 45% carbohydrate, 1% calcium and phosphorus and iodine under 1% (Ratcliffe, 1940, p. 464). The previous diets are mentioned and included polished rice, boiled sweet potatoes and bananas (with green foods, citrus fruits, milk, and eggs for apes), although nutritional values are not given. For primates, Ratcliffe notes that half of the energy intake came from the manufactured mix, supplemented with uncooked fruits and vegetables (sweet potatoes, carrots, apples, bananas, citrus fruit, and green vegetables). In addition, anthropoid apes were given 1 to 4 litres of fresh whole milk daily. Differences were also noted for gorillas, who were given uncooked ground horsemeat daily and 200 grams of boiled horse liver 3 to 4 times a week. Along with mentioning a variation for some specific taxa, Ratcliffe also outlines an adjusted diet for pregnant or lactating females, showing awareness of the changing needs of the animals at different life stages.

The pattern is repeated for herbivorous and carnivorous zoo cake. Of note is that herbivorous diets were modified versions of manufactured feeds already designed for cattle and sheep from the influential work of F.B. Morrison, highlighting the influence of agricultural nutrition on early zoo nutrition (Ratcliffe 1940). Ratcliffe's diets were designed to be adapted to the requirements of a zoo, whilst knowledge of animal preference, and known wild food habits were considered. They were designed to be easy to be prepared by zookeepers, and saw the reduction of individual food items into one hardened mixture to be divided between the animals as needed. Overall, Ratcliffe viewed the new diets to be acceptable to the animals, adequate for their nutritional needs and, importantly, financially beneficial for the zoo (Ratcliffe, 1940, p. 471).

Zoo cake as a result was the first manufactured, "complete" feed for zoo animals. It was designed under the auspices of uniformity and efficiency, a universal tool to improve the health and well-being of zoo animals in a cost-effective manner that delivered essential minerals and vitamins easily. Historically, this was not an innovation that happened in a vacuum. Complete feeds were explored within human nutrition at this time and can be traced back into the latter half of the 19th century (Haushofer, 2023). Manufactured feeds for domestic pets were also explored around this time with Spratt's Dog Biscuit considered the first manufactured pet feed developed from the 1860s and canned dog food coming to the market in the 1920s (Grier, 2009).

Ratcliffe celebrated zoo cake as a primary reason for the improvement of the health and well-being of zoo animals at Philadelphia Zoo. This served as a key element in a special issue on nutrition within the new zoo journal, the International Year Zoobook. In this issue, Ratcliffe's promotion of zoo cake and manufactured feeds came head-to-head with the opposing philosophy of the father of zoo biology, Heini Hediger – a clash of great zoo minds that would influence the rest of the 20th century and approaches to feeding zoo animals (Lane-Petters, 1966).

Philosophical differences: The 1966 Debate

The 1966 debate is one of clashing epistemic positions and philosophical approaches of zoo scientists from different scientific backgrounds. On the one had there is the promotion of

manufactured feeds by pathologist Herbert Ratcliffe, supported by Hans Wackernagel (Scientific Advisor at Basle Zoo at the time), Heini Hediger, the zoo biologist and director of Zurich Zoo who argues for a more natural approach to feeding, and Ralph Fiennes, pathologist at London Zoo. Whilst Fiennes tries to provide a neutral approach to the competing ideas of natural versus manufactured feeds, he largely supports the need for a manufactured feed due to his view that natural feeding is impossible within a zoo and fresh food items are far too unreliable in nutrient composition. The positions of the pathologists versus the zoo biologist provide a metaphorical and literal difference of standpoint, with the pathologists drawing on knowledge from the internal animal and the zoo biologist using their experience of looking *at* the animal as opposed to in. It is also a debate that still holds significance in the present day: several zoo nutrition experts interviewed for this research highlighted its importance and indeed some slight reservation that zoo animal nutrition no longer entertains such collegiate disagreements.

The debate is staged by Willian Lane-Petter (a former director if the British Laboratory Animals Bureau) as a topic of significant importance, delivered by zoo scientists of global importance. Lane-Petter's attempts to situate the debate neutrally fail, however, as his narrative is one that questions the zoos' ability to provide a natural environment and natural behaviours for zoo animals. Lane-Petter's introduction places the weight of the argument on Hediger to demonstrate how a zoo can care for an animal naturally, challenging the idea that naturalness can exist within the zoo (Lane-Petter, 1966), pointing out that for a zoo to care for an animal naturally would require a deliberate zoo policy of nutritionally deficient diets to mimic wild animal experiences. In support of manufactured feeds, the point is made that more had to be done to alleviate nutritional deficiency in zoo diets and that this can only be achieved through manufactured feeds where the nutritional composition is known and as guaranteed as possible (Lane-Petter, 1966). This is an argument supported by Ralph Fiennes, who whilst attempting a neutral position largely agrees with Ratcliffe's zoo cake. Fiennes argues that the unpredictability of nutritional composition of 'natural' foods means it is difficult to rely on natural feeding regimes to maintain the animals health (Fiennes, 1966). Essentially the debate becomes Heini Hediger's belief that zoo animals should be cared for and fed in a way that is as natural as possible versus the voices of Ratcliffe and Wackernagel arguing for importance of the internal animal health above all else.

Whilst the debate includes several zoo scientists, the essence of this difference of opinion rests on the two main protagonists, Heidger and Ratcliffe, both of whom take different approaches to expressing their opinions on feeding in the modern zoo. Ratcliffe largely repeats his arguments he had made nearly 20 years earlier when he introduced the zoo cake recipe. His 1966 paper introduces two entangled points, the risk of animal disease and that disease can be prevented via proper nutritional provision (Ratcliffe, 1966). The core difference to his previous publications is the citing of data to support the zoo cake approach. For example, Ratcliffe identifies the success by showing that tuberculosis in birds reduced due to improved quality of protein. Furthermore, Ratcliffe notes that resistance to dysentery bacilli by non-human primates increased within 8 weeks of the introduction of the new diets (Ratcliffe, 1966). Additionally, the statistics of mortality rates for mammals and birds at Philadelphia Zoo are included covering a period from 1908 to 1964. These figures identify that two years (1937) after the introduction of new diets rates of death began and continued to decline. The argument is that simply changing diets to include manufactured feeds was integral in reducing the effects of disease and thus death within the zoo collection. Ratcliffe acknowledges the need for feeding to encourage natural behaviours but does not specify how this happens with the zoo cake diet. Furthermore, the imagining of the zoo animal by Ratcliffe is one of a docile, subordinate and cooperative body. Addressing concerns over animal acceptability he merely notes that resistance to the diets was only manifested by the zookeepers (Ratcliffe, 1966). His situating of the zoo animal is as an

object, with knowledge and success informed by death, as opposed to the lived experience and observation of the zoo animal (Moore, 2024).

Hediger uses his paper to systematically pick at the zoo cake approach and Ratcliffe's arguments. Broadly, Hediger presents two key concerns; firstly, the risk of domestication of zoo animals through restrictive feeding practices that do not allow natural behaviours or support their holistic health, including psychological and physiological needs. Secondly, that the improvement in zoo animal health in the early 20th century is not only due to with what or how animals were being fed. For example, Hediger raises the point that during the period of Ratcliffe's results, there had been vast innovation and development in enclosure design, veterinary pathology and husbandry practices (Hediger, 1966). Hediger notes that despite the reduction of some diseases within zoos, there were increases in others, such as arteriosclerosis. He (selectively) uses the commentary and experiences of other zoo professionals (T.H. Gillespie of Edinburgh Zoo and Lee Crandall of the Bronx Zoo) in his attacks on manufactured feeds. However, Hediger's primary concern is not that other zoos achieved similar results as Philadelphia without running a manufactured feed regime or that new diseases were introduced to the zoo, but that the zoo cake approach risked sending zoo animals towards domestication. Hediger expressed his concern for the monotony zoo cake introduced to the animals life, and deep concerns over the influence of agricultural knowledge, such as F. B. Morrisons work, stating that "*in zoos we do not want fast growing protein suppliers, economic food producers or animals for fattening; nor do we want to have anything to do with abstract races of animals reared for domestic or agricultural purposes*" (Hediger, 1966, p. ?). Hediger gives the example of a tiger who arrived at Zurich Zoo from Philadelphia unable to tear meat from the bone, commenting that a tiger who does not know how to tear up meat is no longer a tiger (Hediger, 1966). This aligns with Hediger's deepest fear that zoo animals will become domesticated and caricatures of their wild counterparts through manufactured feeding programmes, and he calls on zoo biologists to avoid this by rejecting manufactured feeds (Hediger, 1966).

Hediger's perspective comes from his work observing zoo animals in captivity and their wild counterparts in their natural habits (de Bont, 2024). Innovation at the zoos Hediger was involved with largely came from his experiences of field studies outside of the zoo, such as the concrete termite mound built at Basel Zoo in the zebra enclosure (de Bont, 2022). Hediger did not necessarily see a demarcation between the zoo animal and the wild animal, instead arguing that each maintained predictable behaviours (de Bont, 2022), meaning the zoo animal was only lacking quantity of space and not freedom as is implied by captivity, and that to ensure their physiological and psychological health this needed to be quality space in a new environment (Chrulew, 2014).

The Nutritional Turn

The Nutritional Turn is a period I have assigned to the late 20th century into the early 21st century that is highlighted by a handful of conferences and events that consolidated the work of Ratcliffe and Hediger. They show the movement of the science and practice of zoo feeding drawing closer together. This section will focus on the Dr Scholl Nutrition Conferences held at Lincoln Park Zoo between 1980 and 1991, and the first European Nutrition Research Group conference held at Rotterdam Zoo in 1999. These conferences were pivotal for two reasons; firstly we can see in the topics discussed a balancing of zoo feeding from the scientific perspective and a focus on the animal both internally *and* externally. Secondly, they hallmark the development of the role of the zoo nutritionist within zoos in Europe and the US. It is in this period that nutritionists are employed by zoos and specific nutrition programmes are launched (Crissey, 2001). Dr Olav Oftedal would be the first, hired by Smithsonian's National Zoological

Park in 1978, with the Philadelphia Zoo hiring its first zoo nutritionist in 1984. Furthermore, nutrition programmes were launched in the US and Europe during the 1980s and 1990s at zoos such as Toronto, Rotterdam, Brookfield Zoo, The Wildlife Conservation Society, Dallas Zoo, Fort Worth Zoo, San Diego, the Durrell Wildlife Conservation Trust, and at the Royal Zoological Society of Scotland (Crissey, 2001). At the turn of the millennia there were 15 full or part-time zoo nutritionists in Europe (van Wees et al., 1999). The pace of zoo nutrition at the time is evident in the conference programmes, and employment of zoo nutritionists. Whilst it is questionable how far the professionalisation of the zoo nutritionist role has since progressed, the nutritional turn of the late 20th century can be identified as a significant era of zoo nutrition as an applied science just 80 years after its establishment.

The nutritional turn began with the first Dr Scholl conference in 1980, bringing together zoo scientists, academics, veterinarians, nutritionists, feed manufacturers, zookeepers, and zoo directors to scientifically explore the diverse and varied problems of feeding and nutrition in the modern zoo. Over its nine years, Dr Scholl Conferences featured 136 papers or discussion groups ranging from detailed analysis of nutrient composition, species-specific research and more general and practical measures and practices of zoo feeding. These conferences provide a historical bridge between the clashing philosophies of the 1966 nutrition debate and the more balanced, science and practice informed approaches of 21st century zoo nutrition science. The inaugural conference started with a justification, arguably a defence of zoo cake and Ratcliffe's work at Philadelphia. Wilbur Amand, senior veterinarian of Philadelphia Zoo, extolled the virtues of the system, mentioning that it was still being used with minimal adjustments from Ratcliffe's design. Although he did acknowledge that some manipulation of the facts had taken place, although Amand defended this by stating; *"I think the facts were manipulated a little bit, not necessarily to sell a product but to sell a concept of philosophy. Still, I think the concept/ philosophy was good"* (Amand, 1980, p. 24).

The first conference kept to the Ratcliffe philosophy, focussing primarily on the animal as a scientific object, the processes inside the body and largely not addressing the lived experience. Out of the 20 papers at this first conference, all provide knowledge gained from the inside of animals. Only in snippets, such as Dennis Meritt's (Assistant Director of Lincoln Zoo) recommendation of *"speaking softly to a new arrival, in its native tongue"* (Merritt, 1980, p. 59) are the lived experience or the human-animal relationship visible. However, the journey to a more balanced approach did not take long to emerge and this is where we see the balancing of Ratcliffe's science objects and Hediger's science subjects combine.

Mary Allen, a research scientist at Michigan State University, delivered a concise overview of manufactured feeds with more "natural" feeding options – described as cafeteria style feeding. The paper does not promote a particular approach but identifies the pros and cons of each approach; manufactured feeds may provide guarantees around nutritional value for the animal, but they also limit natural behaviours. Cafeteria style feeding elicits these natural behaviours allowing visitors and zookeepers to observe the animal eating and enjoying variety. However, using the example of an orange and elephants, Allen cautions against the concept of naturalness of the cafeteria style, noting that just because something is fresh or naturally grown does not mean it is appropriate or connected to the animal's wild diet (Allen, 1982, p.2).

Furthermore, Allen highlights issues related to hierarchies and nutritional wisdom of captive animals and the risks of over or under consumption, albeit acknowledging tha providing medication is easier with fresh food. The key message from Allen is that the approach taken for feeding zoo animals should be centred on the animal as much as possible, rather than the historically human-centred approach of 19th and early 20th century zoos. Along with this paper from Allen, Terry Maple, animal behaviourist, presented on the need to ensure behavioural needs are met as well as nutritional for zoo animals, and Allen again with Bonnie Raphael presented on

implementing and managing nutrition plans in zoos. Ellen Dierenfeld, zoo nutritionist, encapsulated the debate and where zoo nutrition had moved to in the twenty years since the *IYZB* debate at the 7th Dr Scholl conference. Dierenfeld, in hindsight, presented a paper that was largely prophetic in the need for zoos to engage with zoo nutrition science and the changing landscape of the late 20th century zoo. The Dr Scholl conferences were not only important because of the broadening of topics discussed but also because of what they launched: from these conferences, the Comparative Nutrition Society and the Nutritional Advisory Group (NAG) were founded. The conferences also led on to the first European nutrition research group conference at Rotterdam in 1999 (Dierenfeld, personal correspondence, 2022).

The change in content at the Rotterdam conference is evidence of the changing nature of zoo nutrition science, zoo feeding, and indeed the increased levels of knowledge of zoo animals and their wild counterparts. 42 papers were presented across several key areas of zoo feeding, organisms, behaviour/feeding ecology, methods, and application. With an historicised sociological lens, we look at the key presentations of this conference to see how far zoo nutrition had travelled since Ratcliffe's zoo cake and the 1966 debate. Susan Crissey presented on the establishment of NAG and the need to understand not just the science of nutrition but also the practice of nutrition. In Jean-Michel Hatt's paper there is a clear move away from the formative years of zoo nutrition debate, acknowledging the developing importance of conservation issues, the improvement in "substitute diets" and the changing perspectives on the value of domesticated animal nutrition for zoo animals (Hatt, 1999).

A snapshot of zoo nutrition science in Europe is provided by Sofie van Wees who noted that in European zoos, the nutritionist was still a luxury with only 20% of zoos employing one and despite only 28% undertaking nutrition research, 83% believed there was a need for additional nutrition research (van Wees, 1999). A situation that I suspect is still present today, and should be empirically assessed, along with a study looking at the types and depth of nutrition research.

These conferences were pivotal in launching what can be seen as an attempt to institutionalise zoo nutrition, an attempt which arguably has not succeeded. 25 years on from the end of the first nutritional turn and the undoubted increased interest in zoo animal nutrition science – where does the field now stand?

Discussion: The Ark Diplomat and present-day zoo nutrition

The perspective on the history of zoo animal nutrition as an applied science depends on the knowledge backgrounds of individuals, informed by their social, cultural, historical and educational experiences, and roles within the zoo. On the one hand, in less than a century, the knowledge created, the methods trialled, the research completed, the journey taken, has been immense. Zoo animal nutrition in the 21st century is far removed from the Philadelphia Zoo pathologists fighting disease and death. On the other hand, despite evidence-based research, some animals are still being fed incorrectly in managed care, both from a nutritional and behavioural viewpoint. One interviewee for this research was exasperated that a zoo association report found animals as familiar as the giraffe were still being fed incorrectly after nearly two centuries of managed care. My personal experience was one of surprise whenever I came across primates that included fruit. The scientific evidence is clear on the benefits of moving away from cultivated fruit in captive primate diets (Plowman and Cabana, 2019), as supported by the majority of EAZA best practice guidelines for primates which advise against fruit feeding – yet it continues, even within some scientifically focused zoos.

Zoo feeding is an emotive subject, it is a traditional practice and as much as this paper has charted the scientific debate, there is broader discussion not covered in this paper, the 'art of

feeding'. Furthermore, the simple fact is that the zoo world is very diverse, by country, region, qualifications of staff, legal requirements, expectations of visitors, by their living collections. The "silver bullet" of Ratcliffe's zoo cake is clearly not the answer, the idealism of Hediger equally hasn't worked. Whilst towards the end of the 20th century these approaches combined, the advancement of zoo nutrition has not achieved what it hoped for at the turn of the millennium – despite the efforts of brilliant and ingenious nutritionists, veterinarians, and zookeepers.

As the zoo nutritionist has not successfully institutionalised within modern zoos, peaceful diplomacy is a requirement for success zoo nutrition. Zoo nutritionists are broadly "the ark diplomats" of the zoo world, which is a direct outcome of how zoo nutrition science has developed. This characterisation is drawn from the work of philosopher Isabelle Stengers and applied within a historical lens of the Judeo-Christian salvational imagery applied to zoos in the 1960s. This period was notable for its adoption of conservation aims and the saving of endangered species (Moore, 2024; Margodt, 2010; Chrulew, 2017; de Bont, 2024).[2] The ark diplomat is someone who strives to "give peace a chance" through artificial arrangements that slow potential confrontation, rather than practices of flexible negotiations between parties who are ready to adapt (Stengers, 2010; Janicka, 2023). Furthermore, the ark diplomat must be empowered by those that hold the power (Stengers, 2010). For zoo nutritionists, this empowerment comes from zookeepers and from zoo administrators who approve and enact their reviews of diets and changes to diets. The development of zoo nutrition science during the nutritional turn has placed the zoo nutritionist in this diplomatic role where they are seeking, with other zoo colleagues, to improve the health and lived experience of the zoo animal – albeit this is not always a straightforward or peaceful process.

This research project explored the historical journey of zoo nutrition as an applied scientific field and its rise from Ellen Corsen-White's research through to the nutritional turn of the late 20th century. Not featured as strongly here but ultimately relevant to understanding zoo nutrition science today, this research also investigated the experiences and memories of some of those present during the nutrition turn. Through interviews with persons involved in zoo nutrition science, mostly in Europe, some potential reasons as to why the zoo nutritionist has been forced into the role of ark diplomat can be posited.

The reasons for the stalling of the field could fill a paper itself, but broadly, those who participated in the nutritional turn and led the field identified some key issues with the engagement of zoo nutritional science. Andrea Fidgett, formally nutritionist for Chester Zoo in the UK and Director of Wildlife Nutrition at San Diego Zoo, viewed it as an issue of the lack of robust research and lack of investment. '*I think if truth be told where I feel we're at with nutrition is I think both continents have stalled because I don't know that the science that's coming out of Europe is – I think there's a lot of people just trying to get by doing baseline work. Which is, what are we feeding animals and documenting that because there isn't the investment into doing robust science'* (Fidgett, interview, 2022).

Another zoo nutrition expert questioned whether there is too much agreement and that a return to competing debates such as in 1966 is required. "*Maybe one thing we should get more, let's say, controversial discussions also within the zoo field in nutrition. I think we perhaps to agree a bit too much. I think this clashing of this important people and opinions against each other I think is great and I like that and we should maybe have more of that to get then new things happening from it and new ideas"* (Zoo Nutrition Expert, interview, 2022). This perspective arguably aligns with Fidgett's concern on the lack of investment in robust research.

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[2]The modern zoo era arguably commenced with the opening of Tiergarten Schöbrunn, Vienna to the public in 1765; this was followed by Zoo Jardin des Plantes in Paris in 1794, and London Zoo in 1828 - widely considered to be the first scientific zoo (Fisher, 1967; Marvin and Mullan, 1987; Baratay & Hardouin-Fugier, 2002).

Or Cecile Lyon, a zoo nutritionist, who believes that advocacy is what is missing from the field, that knowledge simply isn't being shared sufficiently. '*We have a lot of knowledge available that still currently isn't being used and there are animals that suffer and pass away because they are not fed the correct diet and that's something that's avoidable"* (Lyon, interview, 2022).

The most obvious example of this is the outcome of the work from Amy Plowman at Paignton Zoo in the 2010s, evidence-based knowledge that shows that zoos should not feed captive primates cultivated fruit. Yet, many zoos continue to feed cultivated fruit, despite Plowman's research and recommendations within EAZA best practice guidelines to not feed cultivated fruit to primates (albeit with differing standards from 'not at all', to 'with caution', to 'only in training').

For others, the solution to revitalising zoo nutrition in zoos is for zoos to be smarter about their approaches. Paul Rose, an animal behaviourist with the University of Exeter, took the view that greater collaboration was needed within the zoo world and outside of it with interested parties (Rose, interview, 2022).

Then there is the human condition. Selecting food items, feeding, eating, feeding other animals is part of the human condition. There is a connection to the act itself, it is a shared experience between human and non-human. Fidgett, for example, highlighted that in designing a diet for an animal there needs to be multiple levels of acceptance – the zoo animal and the zookeeper. "*I often talk about acceptance of a diet knowing that I mean two things. I mean, animal acceptance and care professional acceptance. Because without that reciprocity you're not going to achieve what you're both trying to do – which is make sure the animal has what it needs*." (Fidgett, interview, 2022) However, the challenge in creating this acceptance is a large part of the diplomatic work by the zoo nutritionist. Food relationships influence acceptance of zoo animal diets. This is where the role of zoo nutrition scientist is different to other zoo scientists and deserves greater appreciation, understanding, and support from zoo administrators and zoo leaders. Veterinary science, or reproductive science, for example, are not areas most people without PhDs in those areas have experience of. Everyone eats.

Nutrition science as a result must overcome the experience of being human and sharing experiences that human carers can align with. This diplomacy and navigating isn't something other zoo sciences have to overcome to the same degree. It may also shed some light on why there are more zoo nutritionists in North America. Eating manufactured feeds, zoo cake, kibble, is not something humans experience. However, humans globally have been encouraged to ensure they eat 5 fruit and veg a day and the fresh (or natural) food stuffs given to animals in European zoos is known, experienced, understood by zookeepers. Which is why you have situations like zookeepers not giving lion cubs meat on the bone for fear of them choking (Plowman, interview, 2022) or when it was assumed bats had nutritional wisdom and were allowed to choose between fruit and their pellets, resulting in the pellets being left and a calcium deficiency nearly wiping out the bat collection. As Fidgett points out, "*fruit wasn't a source of the vitamins and minerals necessary. You don't eat fruit to get healthy bones"* (Fidgett, interview, 2022).

These issues, conflating shared experiences of eating, the lack of investment in nutrition research, and the lack of debate are examples as to why zoo nutritional science – particularly in Europe – has stalled since its rapid rise in the 20th century.

At the risk of being idealistic, the onus rests with zoo associations, such as EAZA and BIAZA and AZA and zoo administrators themselves. In an age of concern about endangerment of species and the resilience of our planet, the zoo nutritionist is equally endangered and arguably more should be done to integrate the knowledge, practices, and expertise of zoo nutritional science into zoos globally.

Zusammenfassung

Die Tierernährung in Zoos als angewandtes Wissenschaftsgebiet ist etwa ein Jahrhundert alt und hat zu bedeutenden Entwicklungen und Veränderungen in der Fütterungspraxis moderner Zoos geführt. Während die Geschichte der Tierernährung in Zoos innerhalb des Berufsstandes dokumentiert ist, wurde bisher kaum untersucht, wie und warum sich die Fütterung und Ernährung in Zoos verändert hat. Dieser Artikel ergänzt die vorhandene Literatur durch eine historisch-soziologische Interpretation der Entwicklung der Tierernährung in Zoos. Die Tierernährung in Zoos hat sich als angewandte Wissenschaft seit ihren Anfängen im frühen 20. Jahrhundert rasant entwickelt. Die modernen Fütterungspraktiken in Zoos haben sich mit dem Wissen, das durch die Tierernährung in Zoos gewonnen wurde, verändert, aber auch im Einklang mit der Entwicklung der Zoos von Symbolen imperialer Macht zu Orten wissenschaftlicher Neugier und Unterhaltung bis hin zu naturschutzorientierten Einrichtungen, die sich auf die Gesundheit unseres Planeten konzentrieren. Die Ursprünge der wissenschaftlich fundierten Tierernährung in Zoos lassen sich bis zur Arbeit des Penrose Research Laboratory (gegründet 1901) im Zoo von Philadelphia zurückverfolgen. Untersuchungen zu den Todesursachen der Zootiere unter der Leitung von Dr. Herbert Fox ermöglichten die Forschung von Dr. Ellen Corson-White, die einen Zusammenhang zwischen Ernährungsmängeln und Krankheiten sowie Sterblichkeit herstellte. Diese Erkenntnisse wurden von Dr. Herbert Ratcliffe weiterentwickelt, der den „Zoo Cake“ entwickelte – das erste industriell hergestellte Alleinfuttermittel für Zootiere –, mit dem die Ernährung standardisiert und optimiert und gleichzeitig Krankheiten reduziert werden sollten. Die Einführung industriell hergestellter Futtermittel löste eine philosophische und praktische Debatte aus, die durch den Austausch zwischen Ratcliffe und Heini Hediger im International Zoo Yearbook 1966 veranschaulicht wird. Ratcliffe legte den Schwerpunkt auf interne Gesundheitsindikatoren und Effizienz, während Hediger vor Verhaltensverarmung und „Domestizierung” durch künstliche Fütterung warnte. Dieser Konflikt verdeutlichte die epistemologische Kluft zwischen pathologischer Wissenschaft und ethologischer Beobachtung, eine Spannung, die das ganze Jahrhundert über bestehen blieb. In den letzten Jahrzehnten des 20. Jahrhunderts trat die Ernährung von Zootieren in eine Phase ein, die als „Ernährungswende” bezeichnet werden kann. In dieser Zeit gab es Versuche, das Fachgebiet durch Konferenzen wie die Dr. Scholl Nutrition Conferences und das Treffen der European Zoo Nutrition Research Group 1999 zu institutionalisieren. Die Tierfütterung in Zoos integrierte zunehmend Verhaltensökologie und Ernährungswissenschaft. In dieser Zeit entstand auch die Position des Zoofütterers als Angestellter in Zoos, obwohl die Akzeptanz in den Einrichtungen begrenzt blieb. Die heutige Tierernährung in Zoos spiegelt ein ausgewogenes Verhältnis zwischen der evidenzbasierten Nährstoffversorgung und der Förderung natürlicher Fressgewohnheiten wider, das während der Ernährungswende mit traditionelleren Ansätzen entwickelt wurde. Die heutigen Tierernährungswissenschaftler in Zoos sind „Arche-Diplomaten“, die ihre vermittelnde Rolle zwischen Wissenschaft, Tierhaltungspraxis, institutionellen Prioritäten und Tierschutz hervorheben. Obwohl sich das Fachgebiet seit seinen Anfängen im frühen 20. Jahrhundert deutlich weiterentwickelt hat, ist die institutionelle Integration noch unvollständig. Eine größere Anerkennung und Stärkung der Fachkompetenz im Bereich der Zoofütterung ist unerlässlich, um den miteinander verflochtenen Herausforderungen des Tierschutzes, der Erhaltung der biologischen Vielfalt und der Gesundheit unseres Planeten im 21. Jahrhundert zu begegnen.

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DER ZOOLOGISCHE GARTEN

THE ZOOLOGICAL GARDEN

doi:10.53188/zg0045 Zool. Garten N.F. 93 (2025) 137-177

Husbandry, feeding, veterinary aspects, pathological findings and historical survivorship of Indian (*Hystrix indica*) and African (*Hystrix cristata*) crested porcupines in European zoos

Haltung, Fütterung, veterinärmedizinische Aspekte, pathologische Befunde und historische Überlebensdaten von Indischen (*Hystrix indica*) und Afrikanischen (*Hystrix cristata*) Stachelschweinen in europäischen Zoos

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Abstract

Indian crested porcupines (*Hystrix indica*) and African crested porcupines (*Hystrix cristata*) are popular zoo animals in Europe and are kept by a total of around 400 institutions. The aim of this study was to evaluate the husbandry and feeding conditions of these two porcupine species in European zoos in more detail and to collect common disease patterns. To this aim, data were collected from 90 responding zoos. On average, 3.8 ±2.7 porcupines were kept per enclosure, with most zoos (70%) having a combined outdoor and indoor enclosure. The average outdoor enclosure was 164 ±196 m² in size and supplemented by an average 14 ±18 m² indoor enclosure. The most common methods for population control were same-sex groups (39%) and a 'breed and cull' regime (28%). Medical training was practised by only 23% of the zoos. Although according to current knowledge porcupines rarely become ill under human care, there are some typical clinical

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pictures: 22% (n=10) of all clinical cases in this study were skin-related, with half of these skin pathologies being caused by intraspecies aggression. Likely due to improved husbandry conditions in recent years and advances in wildlife medicine, the overall European zoo population of both species showed an improvement in historical zoo survivorship for both adult and juvenile animals. The average estimated porcupine diet consisted of vegetables, pelleted compound feed, cultivated fruits, seeds and cereal products, nuts, and animal products, with an estimated ingestion of about 90 g dry matter of hay or grass. There were substantial differences in the feeding of cultivated fruit, compound feed, animal products and hay: eleven zoos explicitly did not feed any cultivated fruit, while in the remaining zoos the proportion of cultivated fruit in the ration varied from 0.7 to 48% of the total dry matter fed. Only 56% (n=33) of all zoos surveyed fed hay to their porcupines, and in these zoos, the average amount of non-forage items was lower, suggesting that hay ingestion is related to a lower availability of other diet items. 20% (n=11) of the zoos offered non-forage items in excess of the estimated daily intake, leading to the assumption that their animals would not have had to ingest any forages even if offered. The average body mass of zoo-kept *Hystrix* spp. was higher than that reported for free-ranging specimens, which may reflect energy-dense, forage-poor zoo diets leading to obesity. Therefore, cultivated fruit, grain products and low-fibre pellets should not be used. We suggest that zoos should adopt the recommendation to base their diets on high-quality grass hay as a staple forage, supplemented by fresh branches, green leafy vegetables, limited amounts of cultivated tubers, and a high-fibre, mineralized pellet to ensure appropriate mineral coverage. Together with our extensive literature survey, the results of this study can form the basis for husbandry guidelines for these species.

Keywords: *Hystrix*, husbandry guidelines, enclosure design, population, mortality, obesity, nutrition

Introduction

The family of the old-world porcupines (Hystricidae) is divided into two subfamilies, four genera and eleven different species (van Aarde, 1984). The most common species in European zoos are the Indian crested porcupine (*Hystrix indica*), common to south-west Asia (Grzimek, 1979/80) held in 271 zoological institutions throughout Europe (Zootierliste, 2024a), and the African crested porcupine (*H. cristata*), found in parts of central and northern Africa as well as southern Europe (Mori et al., 2013) kept in 129 European zoos (Zootierliste, 2024b).

Their most peculiar and prominent characteristic is their quill-covered back used for defence. Individual quills can reach up to 35 cm in length and are not firmly attached to the body, being often released when puncturing flesh, and leaving a predator covered in quills, inflicting pain and deep wounds. Thus among mammals, porcupines are prominent examples of prey species of the 'defender'/body armour type, in contrast to the more common 'escape' type (Lovegrove, 2001). Porcupines are sometimes persecuted as agricultural pests and are also hunted for food. They are listed as "Least concern" in the IUCN red list (Amori and de Smet, 2016; Amori et al., 2021).

Under human care, *Hystrix* spp. have been reported to live up to 28 years (Weigl, 2005). Apart from parasitic infections (Hosni, 2006; Harrison et al., 2007; Mori et al., 2015a; Mir et al., 2016; Hodžić et al., 2018; Chakraborty et al., 2019; Coppola et al., 2020a, Cavallero et al., 2021,), a few infectious diseases (Jurczynski, 2011; Morandi et al., 2012; Cardeti et al., 2016; Tóth et al., 2017; Cilia et al., 2020; Cambiotti et al., 2021), dental problems (Ecinoso et al., 2023), neoplasia (Palmer et al., 2023) and intraspecific aggression (Švara et al., 2015), few problems of veterinary relevance have been published for *Hystrix* ssp. under human care, and these animals are considered easy to keep (van Aarde, 1985a). The incisors of *Hystrix* spp., as of all rodents, are hypselodont, i.e.

Tab. 1: Overview of the husbandry requirements for porcupines in different countries with a comparison to the zoos examined in this study (Bundesministerium für Ernährung und Landwirtschaft, 2014; Bundesministerium für Gesundheit und Frauen, 2004; Der Schweizerische Bundesrat, 2008).

	Germany	Austria	Switzerland	This study mean ± SD (range; n)
Enclosure size outdoors	20 m^2/pair, 5 m^2 for each additional animal	40 m^2/pair	Outside 40 m^2/pair plus 4 m^2 for an additional animal	65 ± 160 m^2 per animal (4-1372; 79)
Enclosure size indoors	20 m^2/pair, 5 m^2 for each additional animal (unless provided in addition to outdoor)		20 m^2/pair plus 3 m^2 for an additional animal	4.8 ± 5.2 m^2 per animal (0.3-25; 67)
Enclosure type	Outdoor-only with freeze-protected shelter allowed, indoor-only allowed	Outdoor-only with shelter allowed, indoor-only allowed	Outdoor-only allowed, indoor-only allowed	17% (n=14) zoos without indoor enclosures or heated boxes
Enclosure substrate	Soil, sand for burrowing	Soil, sand for burrowing	There must be a burrowing opportunity	5 zoos (of 80) without burrowing opportunity
Structure	Hollowed logs or dens	Hollowed logs or dens	Den for sleeping, visual barriers,	0 zoos (of 77) without shelter/den
Sociality	Pairs or small groups	Pairs or family groups	-	3.8 ± 2.7 animals (1-17; 90)
Diet	Mainly plant material and fresh branches	Fresh plant material, branches, bones with meat	Fresh branches	9 zoos (of 56) not offering branches

they are rootless and 'ever-growing' (van Aarde, 1985b; Ungar, 2010); their growth constantly compensates for wear in naturally aligned teeth, with problems of overshooting growth typically occurring when the physiological occlusion of antagonistic teeth is disturbed (Clauss et al., 2025). With respect to the cheek teeth of *Hystrix* spp., there is less consensus, with some authors suggesting that they are rooted and do not continue to grow after eruption (Ungar, 2010), and others stating that they are rootless with the potential for life-long compensating growth (van Aarde, 1985b). In the case of the latter condition, sporadic problems with cheek teeth, as observed in other hystricomorph rodents with 'ever-growing' cheek teeth such as guinea pigs (Legendre, 2016; Witkowska et al., 2017), can be expected.

Although *Hystrix* spp. are nocturnal in their natural habitats (Corsini et al., 1995; Fattorini & Pokheral, 2012; Mori et al., 2016; Clauss et al., 2021), they adapt easily to a diurnal routine in zoos (Hammer & Hammer, 2016). Due to their large size and unusual body armour, porcupines are popular zoo animals (Hammer & Hammer, 2016). In the last decade, a novel method to display porcupines was presented that increases their appeal by feeding them on an elevated platform (Hammer & Hammer, 2016). To date, no husbandry guidelines exist for these species, but certain minimum requirements are given in the animal protection legislation of individual countries (Table 1).

In their natural habitat, the diet consists mainly of various plant parts such as roots, bulbs, tubers, rhizomes, stems, leaves, flowers, wild fruit, and tree bark, and animal material like bones or insects is sometimes found in the stomach contents and faeces of *H. indica* and *H. cristata* (Hafeez et al., 2011; Akram et al., 2017; Mori et al., 2017; Khan et al., 2021; Mori et al., 2021; Mori et al., 2022; Bounaceur et al., 2024). They are known for often digging for underground storage parts of plants (Shachak et al., 1991; Bragg et al., 2005). There are also reports of wild *Hystrix* spp. as agricultural pests consuming cultivated plants such as potatoes, corn, cereals and watermelons (Alkon & Saltz, 1985; Mori et al., 2017; Khan et al., 2021). Historically, forage such as hay was not mentioned in feeding recommendations for *Hystrix* spp. in human care; rather, a large variety of domesticated tubers, vegetables, fruit and cereals have typically been recommended for these species (Weir 1967; Tohmé & Tohmé, 1980; van Aarde, 1985a; Puschmann, 2004). Together with a comparatively low metabolism (Hagen et al., 2019), the provision of such comparatively energy-dense diet items might lead to larger body masses, exceeding those of animals from undisturbed habitats.

In the present study, we aim to summarize current husbandry and feeding conditions, diseases as well as possible treatments of Indian and African crested porcupines in European zoos in the last decades, including an evaluation of necropsy reports from surveyed facilities as well as survivorship and body mass data. This information is intended as one of the bases for the formulation of husbandry guidelines for these species.

Materials and methods

Data collection: survey and interviews

We sent an online questionnaire by personal E-mail link to all European zoos keeping Indian and African crested porcupines, as identified from Zootierliste.de and Species360's Zoological Information Management System (ZIMS). Information on husbandry practices, veterinary aspects and pathological findings was collected. The questionnaire is presented in Appendix I. We contacted 280 zoos, of which 90 (32%) responded.

In addition, 18 zoos holding these species in Germany, the Nethelands and Switzerland were visited opportunistically and their porcupine husbandry investigated on-site, acquiring the same information as asked in the survey. Further information for this study was obtained in communications with specialist colleagues such as curators, veterinarians and/or keepers.

Data collection: Survivorship and body mass

Data for the historical survivorship analyses was obtained under Species360 Research Data Agreement # 2019-Q3-RR3, and included the dates of birth and death of *H. indica* and *H. cristata* across institutions around the world. We applied data cleaning as described previously for similar datasets (Meireles et al. 2025a), and retained only animals from European facilities for our analysis. The maximum attainable longevity considered in our analysis for both species was 31 years of age, based on the oldest plausible animals in the dataset (29.6 for *H. cristata* and 30.8

for *H.indica*). Any animals above this age were considered errors in recording-keeping and were entirely removed.

Data for body mass of zoo-managed animals was obtained as part of Species360 research data use agreement # 84212 as recorded in the Zoo Information Management System (ZIMS) and stored by Species360 in January 2022. The data was anonymised, indicating only the body mass entered by a zoo and the corresponding age and sex of the animal, but not the identity or the latitude of the reporting zoo. Additionally, the data did not include an indication of the reproductive status of individuals (e.g., whether animals were pregnant), and the effect of pregnancy on potential body mass fluctuations therefore could not be controlled for. Several steps were performed as explained in Meireles, et al. (2025b) to remove outlier entries from the dataset. Data for free-ranging specimens was obtained from the literature (Santini, 1980; Alkon, 1984; Alkon et al., 1986; Pigozzi, 1987a; Pigozzo, 1987b; Alkon & Saltz, 1988a; Sever & Mendelssohn, 1991; Corsini et al., 1995; Sonnino, 1998; Girish et al., 2006; Angelici et al., 2009; Mori & Lovari, 2014; Mori et al., 2015a; Coppola et al., 2020d; Vishnugurubaran et al., 2021).

Calculations and statistics

General data are displayed as means ± standard deviation.

Historical survivorship evaluation and population pyramids: Our approach followed recent analyses for other species (see Scherer et al., 2024 for more detailed methodological discussions; Meireles et al., 2025a). In brief, we analysed the survivorship of juveniles of up to one month and up to one year of age, and the survivorship of animals that had reached one year of age separately. One year of age is about the time of sexual maturity for *Hystrix* ssp. (Mori et al., 2016). The data were analysed using Cox proportional hazard analysis, indicating whether there was a change in survivorship over time (with birth year), and differences between wild-born and zoo-born and female and male individuals (see Meireles et al., 2025a for details). For graphical display, data were divided into birth cohorts (1900-1979, 1980-1999, 2000-2024). For population pyramids, animals were classified as juvenile (<1 year of age), adult (≥1 to 12 years of age) and seniors (≥ 12 years of age; defined as the age from which on fecundity declines).

Diet evaluation: Ideally, diet reconstruction should be based on intake data as well as on the energy content of the various diet items. As accurate intake data requires weighing offered and leftover feed over a period of several days, for the individual diet items and – ideally – for the individual animals, this was not considered feasible for this study. Similarly, nutritional analyses of items used were beyond the budget of this project. Therefore, we opted for an approach applicable to diet surveys (Flores-Miyamoto et al., 2005); such an approach is necessary in the absence of exact intake data, as certain parts of the diet are often offered in amounts that will overshoot the intake capacity of the animals (e.g., when offered for *ad libitum* consumption), especially for forage. This approach is based on the assumption that non-forage items, for which specific weights are provided, are usually consumed in total by the animals, with the rest of the intake capacity filled by forage items. Due to individual differences in appetite and intake capacity, such an approach should not be used to compare individual animals, but can serve as a rough evaluation of different diet regimes of different institutions. We assumed an average daily dry matter intake of 450 g for an individual adult porcupine based on the intake records of Alkon et al. (1986) and Hagen et al. (2019). We assumed the following percentages of dry matter (DM) in fresh matter to calculate the total amount DM offered: hay (untreated as well as pelleted or extruded), hay cobs, nuts, sunflower seeds, pumpkin seeds, cereals, oat flakes, millet, bread, rusks, dry dog/cat food and mineral supplements 90%; rice, pasta and meat (all cooked) 35%; day-old chicks and egg (cooked) 25%; fruits, vegetables, pulses, herbs and grass 15%. Reported amounts in fresh matter were transferred to dry matter using these estimates. If an animal receives less than 450 g DM per day in non-forage items

(fruits, vegetables, compound feed, nuts, seeds and cereal products, animal products and other food components), the part up to 450 g was assumed to be made up of hay or grass, or, if the zoo did not feed these forages, by branches and browse. For institutions that fed more than 450 g of dry matter per animal per day of the non-forage items, the percentage of the items was calculated and transformed to 450 g of dry matter on a proportional basis, and it was assumed that these animals would not ingest forage items.

Body mass evaluation: Our approach followed recent analyses for other species (Garand et al., 2024; Meireles et al., 2025b). In brief, we determined the cutoff for the age from which animals were considered as adult by applying a Gompertz model to the data; thus, the cutoffs for adults were 1.8 years of age for female *H. indica* and male *H. cristata*, and 2.4 years for male *H. indica* and female *H. cristata*; these data suggest that these species tend to continue to grow after having reached sexual maturity. Then body mass was first averaged per individual (using only data above the adulthood cutoff), and then across the means of all individuals; within species, females and males were compared by an independent t-test. The level of significance was set to 0.05, with p-values between 0.05 and 0.09 considered as trends.

Results and Discussion

Of the 90 European zoos that participated in this study, 69 kept *H. indica* and 21 *H. cristata*. None of the participating zoos kept both species.

Reasons for keeping *Hystrix*. ssp. and display strategies

Especially because they are both attractive (with an appearance referred to as 'dramatic' (Martin et al., 2024)) and, due to their peculiar 'armoured' lifestyle, part of education programs, porcupines are popular in European zoos.

Zoos kept porcupines for several reasons; most indicated educational reasons (70%, n=63), to attract visitors (69%, n=62) and because porcupines are easy to keep (61%, n=55). Porcupines were also kept due to historical tradition (47%, n=42), low acquisition and maintenance costs (27%, n=24) the need to fill an empty enclosure (8%, n=7), or due to research (3%, n=3).

Zoos offered various events with porcupines: The most popular was public feeding or keeper talks in 44% (n=40) of all zoos. "Meet the public" took place in 9% (n=8). Behind-the-scenes tours were offered in 6% (n=5) of zoos. Guided tours with a special focus on porcupines were offered in 4% (n=4) of the zoos, with two zoos offering the opportunity to visit porcupines during a nocturnal tour. Events such as feeding the porcupines by visitors (3%, n=3), a special porcupine show (2%, n=2), a scavengers hunt about porcupines (1%, n=1) and Keeper-for-the-day with porcupines (1%, n=1) were also offered. 34% (n=31) of all zoos in the study stated that they did not offer any special events for porcupines.

Displaying porcupines on an elevated platform with minimal fencing, allowing for a particular experience of the animals without visible barriers (Hammer & Hammer, 2016), was used rarely (2%, n=2).

Husbandry

Group structure, population management and mixed exhibits

The average group size was 3.8 ±2.7 individuals (Table 1), and an average group consisted of 1.9 ±1.7 females, 1.5 ±1.2 males and 0.4 ±1.7 individuals of undetermined sex. Four zoos kept only a single porcupine. In the other 86 zoos, a porcupine group ranged from two to 17 animals.

Fewer same-sex groups were kept (twelve all-female and eight all-male groups) than groups of both sexes.

The group size of the porcupine holdings studied reflects the natural social structure: Girish et al. (2006) report two to eight animals resting together in one burrow, and Mushtaq et al. (2010) report 'family groups' as social structure in Indian crested porcupines. In *Hystrix* spp., both parents as well as older siblings take care of the young porcupettes, protecting them as a family unit; offspring stay with their parents for about one year, i.e. long enough to experience at least one litter of younger siblings (Coppola & Felicioli, 2021; Mori et al., 2025). Smaller group sizes ranging from pairs to solitary individuals are also described in the wild; however, the solitary animals are mostly interpreted as looking for a partner (Sever & Mendelssohn, 1991).

Asked about methods of population control, same-sex groups were the most frequently mentioned measure (39%, n=14), followed by a 'breed and cull' regime (28%, n=10), surgical castration of males (19%, n=7), and chemical castration (usually by deslorelin implant in females) (14%, n=5) in all zoos reporting management options. To our knowledge, there are yet no published details of using deslorelin in porcupines. While 17 zoos left the question about population control unanswered, 37 stated that they did not use any of these measures, presumably allowing animals to breed. Given that both parents and older juveniles are involved in the caring for newborn porcupettes (Coppola & Felicioli, 2021; Mori et al., 2025), it can be speculated that not allowing porcupines to breed not only curtails the natural behaviour of reproduction, but also important social behaviours they have evolved.

In three of the ten zoos that used a 'breed and cull' regime, porcupine carcasses were fed to other zoo animals, typically after skinning the carcass. One zoo once fed a culled porcupine to a lynx (*Lynx lynx*) without skinning beforehand, which was not accepted by the lynx. These feedings took place in public and were explained explicitly by use of signs, live narration during the feeding or via social media. Notably, the breed-and-cull strategy was not peculiar to porcupine management at these facilities, but applied to a larger number of different animals.

In 19 of 90 zoos, porcupines were kept together with other species. The most common species in all associations were meerkats in five institutions, followed by guinea pigs in two. Other combinations only occurred once, including northern tree shrew (*Tupaia belangeri*), Prevost's squirrel (*Callosciurus prevostii*), another porcupine species (*Hystrix africaeaustralis*), ring-tailed lemur (*Lemur catta*), lar gibbon (*Hylobates lar*), white-naped mangabey (*Cercocebus lunulatus*), mongoose (*Herpestidae*), Bactrian camel (*Camelus bactrianus*), Vietnamese pig (*Sus scrofa domesticus*), zebras (*Equus* sp.), blue peafowl (*Pavo cristatus*), Eurasian eagle-owl (*Bubo bubo*), Eurasian griffon vulture (*Gyps fulvus*), marabou stork (*Leptoptilos crumenifer*), and various other bird species. Negative effects resulting from socialization were described only in three of these multi-species exhibits: In one zoo, porcupine quills were found sticking in the legs of Bactrian camels; problems with meerkats were described in two other zoos. In one of these, meerkats attacked young porcupines; in the other, there were disputes during feeding, which were easily resolved by separating the species during feeding events. Serious veterinary problems resulting from socialising porcupines with other species were not described in any zoo.

When keeping *Hystrix* spp. together with other species in mixed exhibits, precautionary measures are recommended, ensuring that the species do not get into conflict at feeding stations or do not ingest inappropriate food items targeted to other species. Even for free-ranging porcupines, conflicts with roe deer (*Capreolus capreolus*) at common feeding sites have been reported, with porcupines invariably being the aggressive, attacking party (Lazzeri et al., 2020). In natural habitats, porcupines are known to share their burrows with other species, especially badgers (Mori et al., 2015b; Mukherjee et al., 2019; Coppola et al., 2020b); to what extent this would be possible in a confined management remains to be tested.

Enclosure design

In the absence of husbandry guidelines, legal requirements for the husbandry of zoo animals can be compared to the results of our survey. The legal requirements of Germany, Austria and Switzerland for the husbandry of *Hystrix* spp. are summarised in Table 1. Generally, the requirements noted in this legislation were met.

The average enclosure size was 164 ±196 m² (10-1372 m²; n=79) for outside and 14 ±18 m² (2-100 m²; n=67) for inside enclosures (see Tab. 1 for areas per animal). Thus, the average porcupine enclosure in this study was about eight times larger than required by German, and about 4 times larger than required by Austrian and Swiss minimum requirements (Tab. 1). Saltz & Alkon (1989) measured a mean home range in free-ranging *H. indica* of 1.5 ± 0.4 km² and a nocturnal movement of 2.8 ± 0.7 km; for an undisturbed habitat, Sever & Mendelssohn (1991) documented a similar home range size of about 1.2 km² for a pair. By contrast, these authors documented a smaller home range in agricultural areas (about 0.4 km²), suggesting that the higher food availability limits the necessity to roam. Natural home range sizes are a result of resource density; nevertheless, it is considered desirable to facilitate similar movement rates in zoo animals as compared to free-ranging specimens. Corresponding measurements are lacking in zoo porcupines, but it is reasonable to suspect that the more often, throughout the day, smaller portions of the daily food ration are given at different locations, the more the animals will move around. In this respect, it would be desirable if more zoos would abandon a one-feeding-per-day regime (see below).

Most zoos kept their porcupines in a combination of indoor and outdoor enclosures (70%, n=57); exclusively outdoor keeping without (17%; n=14) or with heated boxes (10%; n=8) also occurred. Indoor-only housing was rarely practised (4%; n=3) (Tab. 1). The question of indoor facilities is regulated differently in the husbandry recommendations of the various countries. Germany requires a frost-free shelter in winter, while Austria and Switzerland only require shelters or sleeping boxes. Haim et al. (1990) report on the thermoregulatory abilities in Cape porcupines (*H. africaeaustralis*), which can regulate their body temperature between 13°C and 30°C when acclimatised to 25°C. Coppola et al. (2019) note that there is no comparable data for *H. cristata* and *H. indica*, but suggest similar abilities in these two species. *H. cristata* also have to contend with temperature differences in the wild, as Italian summers can be distinctively warmer (23.1°C) than the average winter temperature of 6.8°C (Coppola et al., 2022). *H. indica* also experiences strong seasonal temperature fluctuations: Taslim et al. (2022) report average temperatures of 14°C in winter and 35°C in summer. Khan et al. (2021) even report a temperature range of 2°C to 40°C for *H. indica*. There are also reports of wild *H. cristata* and *H. indica* living around freezing point (Prakash, 1975; Osunsina et al., 2010). It has been suggested that the limitation of the range of *Hystrix* species is not set by temperatures, but by seasonal daylight hours; because porcupines, as nocturnal foragers, depend on a certain length of night to find sufficient amounts of food, they may not occur at latitudes where summer nights are shorter than seven hours (Alkon & Saltz, 1988b). In view of the geographical distribution and adaptability of porcupines, no objections can be raised with regard to the temperature at the zoos participating in our survey.

The substrate most often used in indoor enclosures was straw - either alone or in combination with other substrates (63%, n=43), followed by concrete (31%, n=21), wood chips (29%, n=20), hay (15%, n=10), bark (10%, n=7), sand (4%, n=3), tiles (3%, n=2), a rubber mat (1%, n=1) and clay (1%, n=1). In outdoor enclosures, sand (56%, n=44) and topsoil (49%, n=39) occurred most frequently, followed by bark (23%, n=18), grass (15%, n=12), concrete (10%, n=8), stones (8%, n=6), gravel (6%, n=5), clay (5%, n=4), paving (3%, n=2), wood (3%, n=2), straw (1%, n=1), mineral mixture (1%, n=1), silica (1%, n=1) and artificial grass (1%, n=1). Burrowing was not possible for the animals in 4% (n=3) of outdoor enclosures, and not in 2 of the 3 indoor-only enclosures. Thus, the requirements for burrowing opportunities were mostly met. In natural habitats, porcu-

pines dig out burrows or dens, which they occupy with up to eight animals; Girish et al. (2006) estimated that for one burrow, soil of the magnitude of 50-60 kg was moved, and reported that '*a lot of time and energy was expended in burrowing activity*'. Facilitating burrowing behaviour is therefore considered important in porcupine husbandry (Martin et al., 2024). Information on how often porcupines dig new burrows is lacking to our knowledge, but Girish et al. (2006) claim that porcupines preferred to dig fresh burrows rather than occupy those abandoned by other animals. This raises the question whether zoo management practices allow for repeated burrowing activity. Unfortunately, we did not specifically ask about whether zoos regularly 'flattened' their outside enclosures, filling the burrows (while animals are locked into another enclosure), to induce new digging activity by their animals. Possibly, doing this on an annual basis, coupled with a shifting of structural enclosure elements, could represent an important enrichment measure for zoo porcupines that could also invite visitor attention and establish a local 'husbandry tradition'.

The structural elements in porcupine outdoor enclosures included wood or tree trunks (70%, n=54), stones (56%, n=43) and artificial tunnels or caves (48%, n=37). Roots (10%, n=8), plants (9%, n=7), hills (8%, n=6), platforms (8%, n=6) and ponds (8%, n=6)were also used. Concrete (3%, n=2), artificial rocks (1%, n=1), heat lamps (1%, n=1) and metal (1%, n=1) were also found in the outdoor facilities of porcupines. In contrast to the outdoor enclosures, indoor facilities were usually rather poorly furnished. 45% (n=27) of all zoos with indoor facilities explicitly reported that they do not use any structural elements indoors; notably, all of these 27 zoos also had an outdoor enclosure, so that the indoor enclosure might have been considered as a 'den' in itself. Otherwise, tree trunks (41%, n=13) and burrows (22%, n=7) were most frequently used in indoor enclosures. Heat lamps (13%, n=4), rocks (6%, n=2) and plants (3%, n=1) were only used occasionally. The indoor enclosures of 59% (n=38) of all zoos with an indoor facility included a separation option. Since porcupines usually sleep in dens in the wild, and also use these to raise their offspring (Haim et al., 1992a; Corsini et al., 1995; Mukherjee et al., 2019), providing hiding places not only in outdoors but also at least in those indoor enclosures that surpass the typical size of a 'den' should be considered.

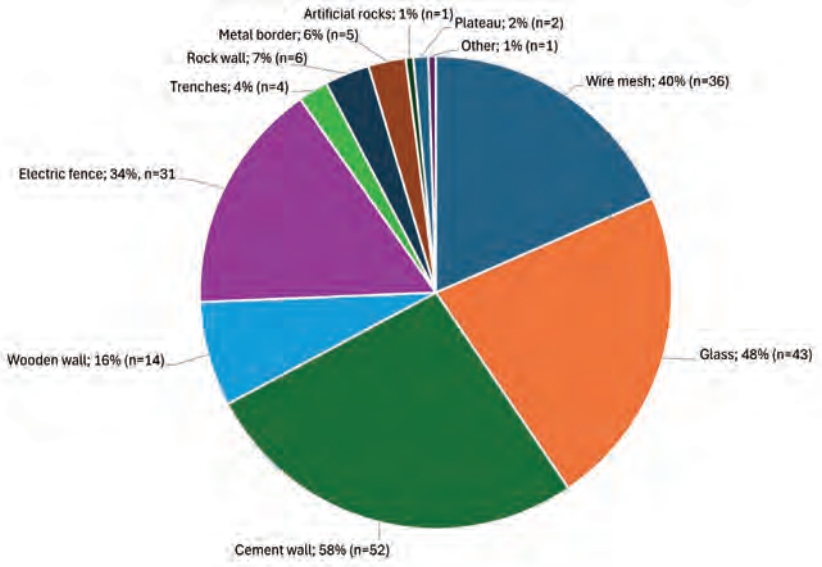

Fig. 1: Used barriers at enclosures of Indian crested porcupines (*Hystrix indica*) and African crested porcupines (*Hystrix cristata*) kept in European zoos.

Various barriers were used for porcupine enclosures (Fig. 1). On average, the lowest point of enclosure barriers was 118 ±77 cm (30-500 cm; n=70). Cement walls (58%, n=52) were most frequently used, followed by glass (48%, n=43), wire mesh (40%, n=36) and electric fencing (34%, n=31). When porcupines are presented on an elevated platform (2%, n=2), no fencing might be necessary due to the animals' fear of heights; however, some barrier that prevents visitors from touching the animals may be necessary (Hammer & Hammer, 2016). Most zoos secured their porcupine enclosures with a burrow protection system (i.e., underground enclosure barriers). Only four of the zoos in the study (5%) explicitly stated that they did not use burrow protection. The most common types of burrow protection used were concrete (34%, n=25), mesh (24%, n=18) and grids (19%, n=14). A deep wall extending into the ground or a deep sunk strip foundation (4%, n=3), (cobble)stones (3%, n=2) and tiles (1%, n=1) were used less frequently. Porcupines are considered escape artists and have already escaped at least once in 30% of the zoos surveyed. The main causes for escaping were climbing over the fence (41%; n=10), digging out (29%; n=7) and human error in the form of incorrectly closed doors (21%; n=5).

Handling and training

93% of the surveyed zoos kept their porcupines in direct contact (n=75), with only 7% (n=6) using indirect contact. However, in 19% (n=15) of the zoos, porcupines had caused injuries to humans. The greatest danger in porcupine husbandry comes from the quills, as 87% (n=13) of all injuries were caused by the quills; in only 13% (n=2) were humans bitten by porcupines. The most common methods of catching porcupines were drift boards (36%; n=32) and catch cages (36%; n=32). Nets (24%; n=22) and distance immobilisation (24%; n=22) were also frequently used. Crate or target training, in which the animals voluntarily enter a transport crate, occurred less frequently (4%; n=4). Medical behaviour training was practised by only 23% (n=19) of the zoos surveyed (Fig. 2). Mainly target training was conducted, but mouth examinations, crate and weighing training were also performed occasionally.

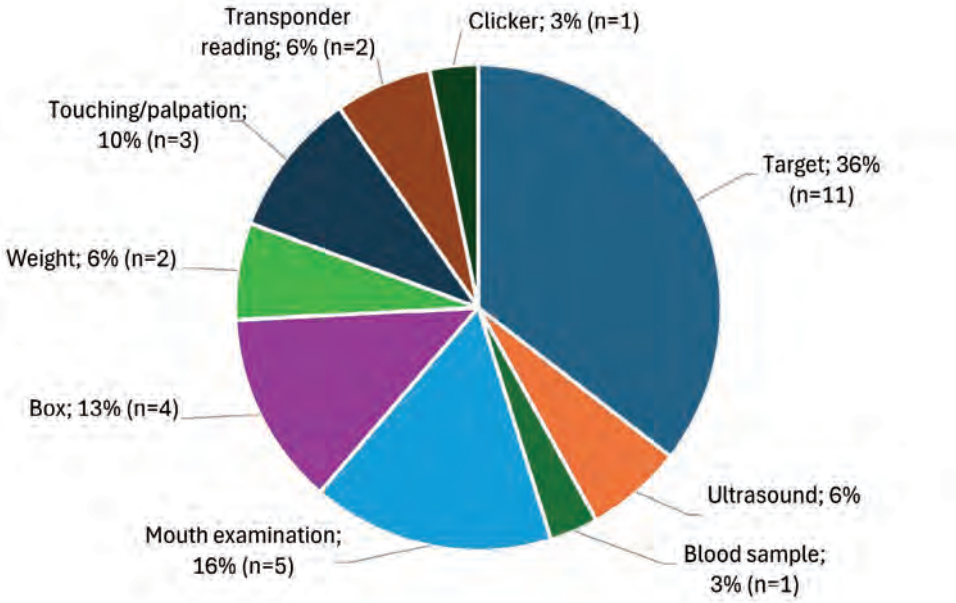

Fig. 2: Medical behaviour training in Indian crested porcupines (*Hystrix indica*) and African crested porcupines (*Hystrix cristata*) kept in European zoos.

Anecdotal information passed on during interviews in the present study, as well as personal observations of some of the authors (MP, MC) support the notion that *Hystrix* spp. will change their behavioural pattern from strict nocturnal activity to diurnal activity under human care (Hammer & Hammer, 2016). Thus, it is possible to present active porcupines during daylight hours. The various reports of training with porcupines support the personal observation of the authors (MP, MC) and a literature review (Martin et al., 2024) that porcupines are used as ambassador animals in training displays in some institutions, and a case report that describes the process by which a porcupine was trained to keep touching a target with its nose for 30 consecutive seconds (Fernandez & Dorey, 2021).

Veterinary aspects

Porcupines seem to rarely get clinically sick in human care: 51 zoos (57%) explicitly reported that they had no health problems in their porcupines. This is consistent with the results of the literature search, where only few porcupine diseases are described. Of the 46 reported medical problems, 22% (n=10) were skin-related, of which half were skin wounds due to intraspecies aggression in the form of bites (Fig. 3). Other frequently affected organ systems were the respiratory tract (20%, n=9), mostly in the form of pneumonia, the teeth (17%, n=8), the gastrointestinal tract (11%, n=5) and the reproductive tract (11%, n=5). Diseases of the eyes (9%, n=4), the musculoskeletal system (7%, n=3) and neurological diseases (2%, n=1) were also mentioned.

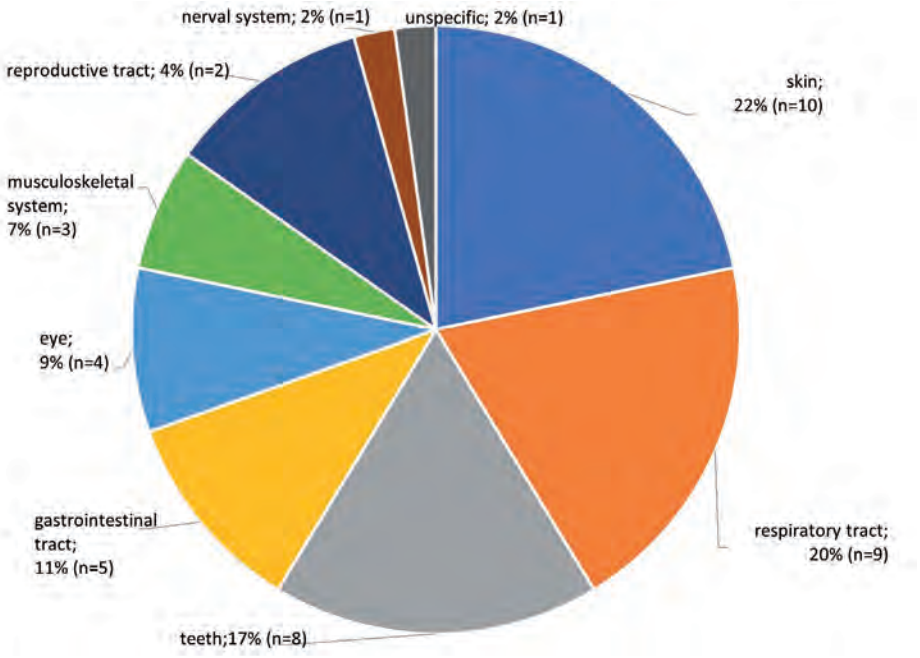

Fig. 3: Affected organ systems in diseased Indian crested porcupines (*Hystrix indica*) and African crested porcupines (*Hystrix cristata*) kept in European zoos.

We received a total of only 31 necropsy reports from 16 zoos, of which nine applied to juvenile animals (<1 year of age) and 22 to adult animals. Evidently, more consistent pathological screening of dead porcupines is recommended. The average age of these animals was 7.7 ±9.2 years; for juveniles, this was 0.2 ±0.2 years (range seven days to five months), and for adult animals 10.3 ±9.3

years (range 1 to 26). In comparison, the median age of adult animals in the most recent cohort of European animals (born between 2000 and 2024) was 15.5 years for the Indian and 14.6 years for the African crested porcupine (Fig. 4).

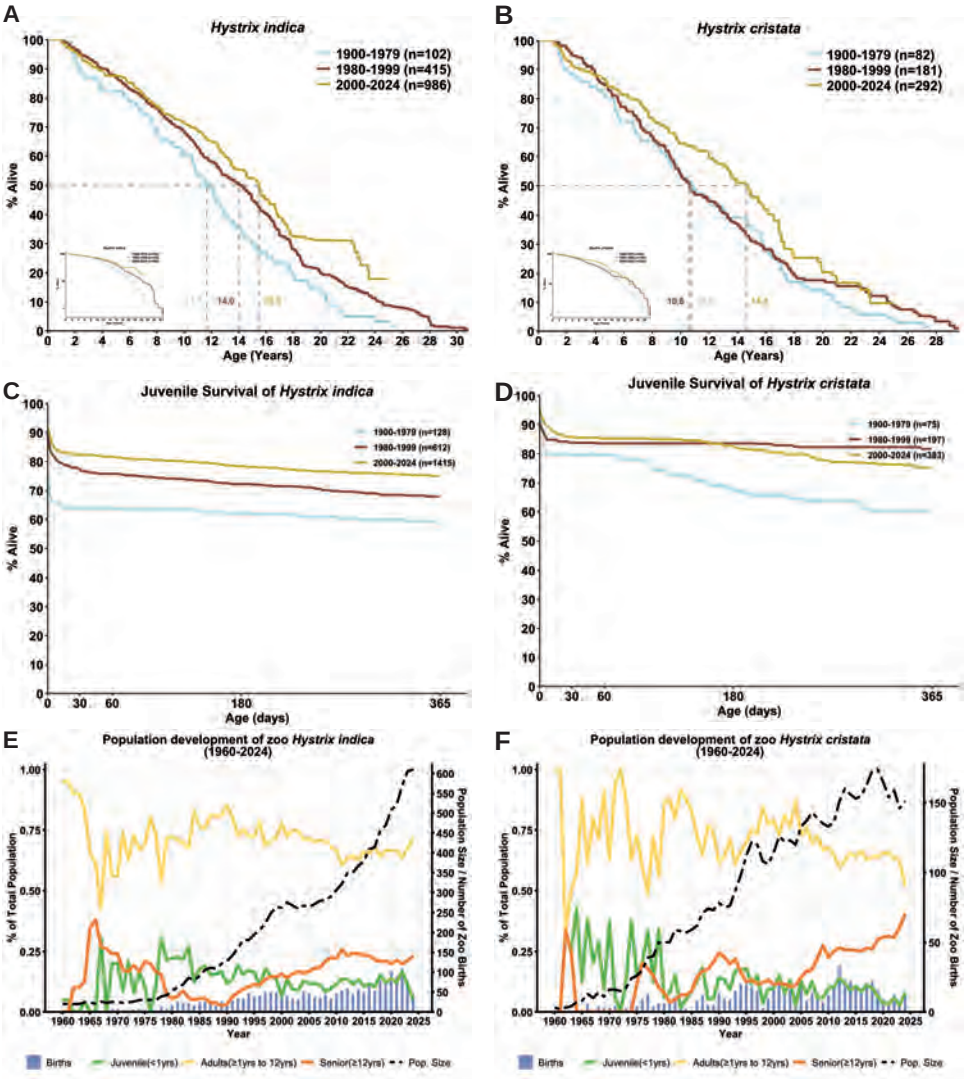

Fig. 4: Adulturvivorship, juvenile survivorship, population development for *Hystrix indica* (**A, C, E**) and *Hystrix cristata* (**B, D, F**). Note the higher survivorship in more recent cohorts, and the increase in senior and the decrease in juvenile animals in the populations.

Cause of death

Among the organs affected in the 25 necropsy reports of adult animals, the respiratory tract was most frequently mentioned at 32% (n=11), followed by the gastrointestinal tract (21%, n=7), neoplasia (9%, n=3), kidney disease (9%, n=3) and the skin (9%, n=3, with 2 cases again being

attributable to intraspecies aggression in the form of bites and puncture wounds). Cardiovascular tract (6%, n=2), neurological pathologies (6%, n=2), reproductive tract (3%, n=1), and sepsis (3%, n=1) played a minor role. Juvenile animals were most frequently affected by cardiovascular problems (27%, n=3) and respiratory problems (27%, n=3), followed by skin problems (18%, n=2) caused by aggression, and sepsis (18%, n=2).

The drugs used in Indian and African crested porcupines and the corresponding dosages are listed in Appendix II; this table also contains literature information on dosages in porcupines.

Infectious diseases

Infectious agents diagnosed in *H. indica* and *H. cristata* by the participating zoos are listed in Appendix III. Only a few bacterial diseases in porcupines have been described in the literature: Porcupines are susceptible to tuberculosis caused by *Mycobacterium pinnipedii* (Jurczynski et al., 2011) and *Mycobacterium bovis* (Cambiotti et al., 2021). Leptospirosis is described in *H. cristata* (Cilia et al., 2020). *Micrococcoides hystricis* was first isolated in 2017 from *H. indica* of Budapest Zoo (Tóth et al., 2017). Kleinerman et al. (2021) detected *Borrelia persica* in wild-living *H. indica.*

Whereas *Aspergillus fumigatus* is the only fungal infection described in this study, there is also only one published case of fungal disease in porcupines: Adiaspiromycosis caused by *Emmonsia crescens* is described in one young male free-living *H. cristata* in Italy (Morandi et al., 2012).

The surveyed zoos had no known problems with viral diseases in porcupines, and only two relevant viruses have been described in the literature to date, to our knowledge: Encephalomyocarditis virus (EMCV) caused myocarditis and asymptomatic deaths with a mass mortality in porcupines in a rescue center during winter (Cardeti et al., 2016). *Paslahepevirus balayani* (hepatitis E virus) is described in free-ranging porcupines, possibly due to sharing the habitat with wild boars (*Sus scrofa*) (Pierini et al., 2021; Pirani et al., 2023); the clinical relevance remains unknown.

41 zoos (46%) stated that they regularly tested for endoparasites (mostly using flotation) but had not yet been able to detect any endoparasitoses in their porcupines. Apart from this statement, we received 85 specific test results from porcupine faecal examinations from eleven zoos, of which 72 (85%) were negative. The most frequently detected parasites were *Trichuris* spp. in ten samples, followed by Strongylidae in three samples and Giardia and Flagellates in a single sample each. Similarly to our study, parasitic problems appear to be rare in porcupines under human care in the literature. *Trichuris* spp. and Ascarids were diagnosed in captive Indian crested porcupines in a small zoo in India (Mir et al. 2016). Rivero et al. (2022) found that *Trichuris* spp. isolated from zoo-housed porcupines had a high similarity with *Trichuris landak* and mentioned *Trichuris hystricis*, *Trichuris lenkorani* and *Trichuris mettami* as the other most common *Trichuris* species in porcupines. Varadharajan (1999) detected *Toxocara* sp., *Strongyloides* sp., Strongyle eggs and *Trichuris* sp. in zoo-housed Indian crested porcupines. Durette-Desset (1966) found two new Trichostrongyles in crested porcupines living in a Vietnamese zoo: *Longistriata levanhoai* and *Longistriata cordicauda.*

In free-ranging specimens, more endo- and ectoparasitoses are diagnosed compared to zoo-housed porcupines, probably due to veterinary surveillance and high standards of hygiene under human care. Self-medication of porcupines by deliberately ingesting plants with antiparasitic properties has been suggested (Viviano et al., 2022). *Linguatula serrata* plays an important role as a zoonotic parasite in *H. indica* in the Middle East (Rajabloo et al., 2015) but does not occur in animals kept in European zoos, possibly due to a lack of intermediate rodent hosts. *Toxoplasma gondii* can cause neurological symptoms in *H. cristata* (Harrison et al., 2007). Coppola et al. (2020a) detected gastrointestinal strongyles, *Trichuris* spp., *Capillaria* spp., *Giardi* spp., *Giardi duodenalis*, Coccidea and *Cryptosporidium* spp. in free-ranging H. *cristata* in Italy. *Trichuris* spp. were also described in free-ranging *H. cristata* in Italy (Poglayen et al., 2005; Coppola et al., 2020c; Cavallero et al., 2021; Viviano et al., 2022) and in free-ranging *H. indica* in Iran (Youssefi et al., 2010). *Archeostrongylus italicus* was de-

scribed repeatedly in wild-living porcupines in Italy (Biocca & Ferretti, 1957, Poglayen et al., 2005, Viviano et al., 2022). *Trichostrongylus orientalis* was found in free-ranging *H. indica* in Iran (Ghadirian & Arfaa, 1972). Chakraborty et al. (2019) described *Dipylidium* sp. and *Parascaris* sp. in wild-living Indian crested porcupines in India. Furthermore, porcupines are susceptible as accidental hosts to *Echinococcus ortleppi* (Hodžić et al., 2018) and to *Trichinella* spp. (Hosni, 2006) as well as for *Taenia twitchelli*, which was found in porcupines' lungs and has zoonotic potential (Yarto-Jaramillo, 2015).

Fleas and ticks are the most seen ectoparasites in wild-living African crested porcupines in central Italy: *Pulex irritans, Ixodes ricinus, Rhipicephalus bursa, Pholeoixodes hexagonus, Ixodes ventalloi, Paraceras melis, Ctenocephalides canis, Dasypsyllus gallinulae* and *Hystrichopsylla talpae* (Mori et al., 2015a). Parola et al. (2005) described *Pariodontis riggenbachi* in porcupines. Viviano et al. (2022) found *Ixodes ricinus, Pholeoixodes exagonus, Pulex irritans, Dasypsyllus gallinulae, Paraceras melis, Ctenocephalides canis* and *Hystrichopsylla talpae* in wild-living African crested porcupines in central Italy with different prevalences during the year. A traumatic myiasis caused by *Calliphora vicina* was described in a porcupine by Scaravelli et al. (2017).

The endoparasite prevalence of 15% in this study is significantly lower than in other retrospective parasite studies in zoo-housed porcupines and other species, where it is usually between 31.1 and 68.3% (Lim et al., 2008; Fagioloni et al., 2010; Barbosa et al., 2020; Murnik et al., 2024). Possible reasons for this are the lower animal density in porcupine husbandry or better hygiene standards in porcupine husbandry. Since many zoos detect endoparasites using flotation and the sensitivity of this test depends, among other things, on the skill of the person performing it, differences in the sensitivity of the diagnostic method used could also be a possible reason for the varying prevalence.

Non-infectious diseases

Dental problems were among the more prominent non-infectious diseases in this study, which align with the literature. In free-ranging African crested porcupines, dental abnormalities are rare (Angelici & Luiselli, 1999). In zoo animals, excessive growth of incisors has been described without a clear indication of the prevalence (Yarto-Jaramillo, 2015). This has been linked to the fact that rodent incisors are 'ever-growing', and it is assumed that any cause leading to malocclusion and/or a lack of a fibrous diet that 'keeps incisors from overgrowing' are responsible (Yarto-Jaramillo, 2015, Martin et al., 2024). However, given ample evidence that the growth of such incisors is controlled by pressure of the antagonist tooth irrespective of the abrasiveness of fibrosity of the diet (Opsomer et al., 2025), malocclusion is the most likely etiopathology – which might be caused by dietary factors unrelated to the diet's abrasiveness but linked to its content of fibre and easily digestible carbohydrates (Clauss et al., 2025). Neither the present study nor the literature report cheek tooth overgrowth in *Hystrix* spp. as found for example in guinea pigs (Yarto-Jaramillo, 2015), favouring the view that *H. indica* and *H. cristata* cheek teeth are not ever-growing (as opposed to a literature report on *H. africaeaustralis*, van Aarde, 1985b). Wolters & Foreest (2003) described a root abscess in the mandibular molar of an African crested porcupine that was treated by extraction of the affected tooth, and after six weeks, the maxillary antagonist had not overgrown, supporting this view; by contrast, Angelic & Luiselli (1999) report the lack of a maxillary premolar in a *H. cristata* skull that evidently led to overgrowth of the corresponding mandibular premolar. Computed tomography images of *H. cristata* skulls (Encinoso et al., 2022; Bordon et al., 2024) do not provide a conclusive answer as to whether these teeth have roots or not (and note that the latter authors also describe the basis of the incisors as 'roots'). Given the large number of *Hystrix* porcupines available across European zoos, a more detailed, conclusive examination of the nature of their cheek teeth to resolve the question whether they are rooted or rootless (and hence, have the capacity for compensating growth throughout the animals' lives), would be welcome.

With respect to intra-specific aggression, one Indian crested porcupine died in a Slovenian zoo after fighting with a conspecific due to a puncture injury that perforated the chest and led to septicemia (Švara et al., 2015). Management practices to regulate animal density in an enclosure, offer a sufficient number of feeding location and structural elements to allow animals evading each other are likely important to reduce intra-specific aggression.

Skin lesions can otherwise be iatrogenic due to trauma by distance injection (Yarto-Jaramillo, 2015). Skin lesions are best sutured with thin threads with atraumatic needles, comparable to material used in avian medicine (Yarto-Jaramillo 2015). To detect the cause of a neurologic disease an MRI can be performed. Anatomical areas of healthy porcupines are described in MRI by Morales-Bordon et al. (2023). Neoplasia in porcupines is rarely described in the literature and was rare in this study; Palmer et al. (2023) reported four cases of mammary adenocarcinoma in zoo-housed Indian crested porcupines.

Historical survivorship

Both Indian and African crested porcupines have shown rapid population growth in European zoos since 1960, although the latter has been declining slightly for the past five years (Fig. 4). In

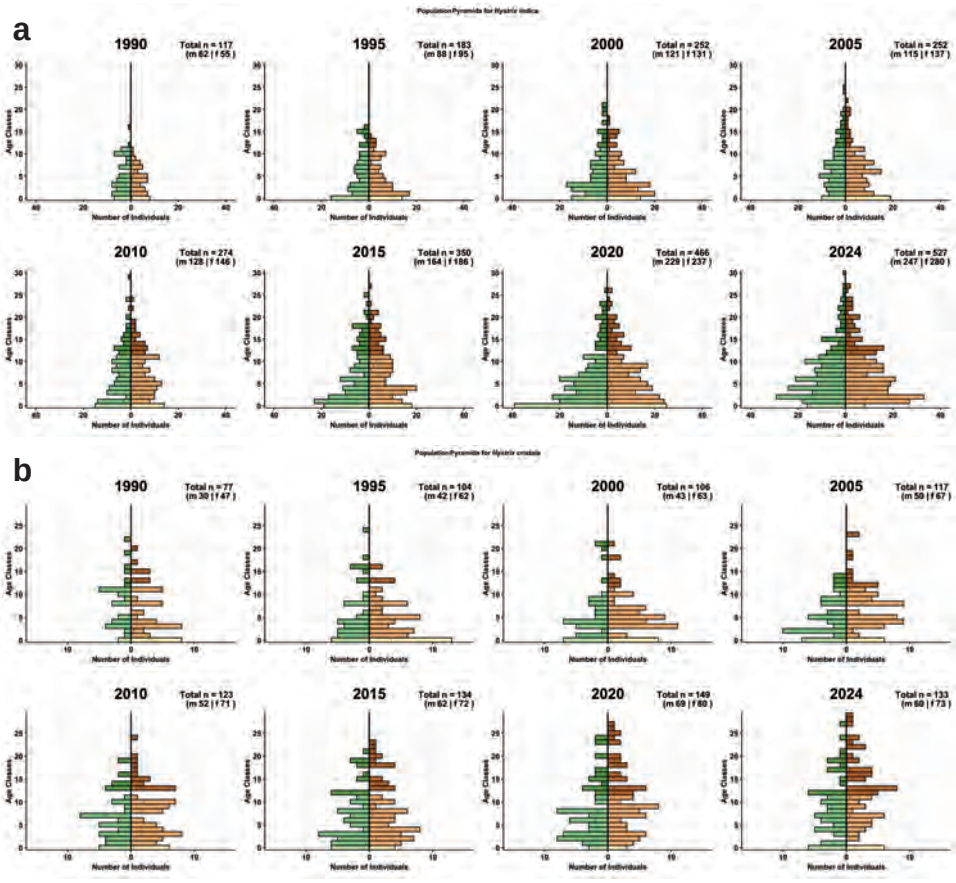

Fig. 5: Population development for *Hystrix indica* (**a**) and *Hystrix cristata* (**b**) displayed as population 'pyramids'. Note the recent development towards a columnar shape in the *H. cristata* population.

both species, the proportion of senior animals increased and that of juveniles decreased, with the trend being more distinct in the smaller population of the African crested porcupine (Fig. 4). The 'population pyramid' consistently had an (expanding) pyramid shape over time in *H. indica*, but a more distinct columnar shape in *H. cristata*, corresponding to the decreasing population size in the latter (Fig. 5). A recent decline in births was evident in both species.

In both species, the graphical display of the survivorship of birth cohorts in adults and juveniles (Fig. 4) suggests improvements over historical time. For both species, the survivorship plots indicated a type I survivorship curve (Deevey, 1947) with an overall low mortality (Fig. 4A,B inlets). This is typical for long-lived mammals that give birth to precocial young that are not exposed to distinct predation. In *H. cristata*, the historical improvement failed to reach statistical significance; in adults, birth year just showed a corresponding trend (n=402, z=-1.71, p=0.087), and there was a numerical increase in the median lifespan of adult animals from 10.6 to 14.6 years. No significant historical trend resulted for the juvenile first month (n=656, z=0.118, p=0.906) and first year (n=656, z=1.145, p=0.252) survivorship. In all these cases, there was also no significant difference between males and females. In *H. indica*, some of the visual trends were significant. For adults, birth year again only showed a corresponding trend (n=1207, z=-1.87, p=0.061), and there was a numerical increase in the median lifespan of adult animals from 11.7 to 15.5 years. In juveniles, the historical improvement of survivorship was significant for the first month (n=2158, z=-5.20, p<0.001) and first year (n=2158, z=-5.07, p<0.001) survivorship. While there was no significant difference between males and females for adult and juvenile first month survivorship, males were less likely to survive until one year of age than females (n=2158, z=2.69, p=0.007). It is difficult to pinpoint any specific husbandry measure to this progress. Similar results have also been demonstrated for other species such as African and Asian elephants, giraffes, and pygmy hippopotamuses (Scherer et al., 2023; Scherer et al., 2024; Meireles et al., 2025a). The lower positive improvement in juvenile and adult survivorship in *H. cristata* and the slight decline in this population over the last five years may be due to the clearly smaller population size in Europe and to the more pronounced obesity (see below), which is very common in the majority of individuals.

Whereas the European zoo population of *H. indica* is thriving, with a robust pyramid-shaped population structure, that of *H. cristata* appears less resilient with a columnar population structure (Fig. 5). The greater variation in the number of adult *H. cristata* over the years can be attributed to the smaller population size, as no differences in veterinary and pathological characteristics were found between the two porcupine species studied. As neither species is classified as endangered, no re-introduction programs are foreseen even in the mid-term future, and no clear differences between the species seem to exist that would lead to differences in their educative value, it might be advisable for European zoos to focus on the *H. indica* species and phase-out *H. cristata*.

Dietary management and body mass

Detailed data on porcupine feeding was available from 56 zoos. The majority of zoos (64%, n=36) fed their porcupines once per day, 25% (n=14) offered food two times, 5% (n=3) 3-4 times, and another 5% (n=3) gave food at a higher frequency multiple times across the day. Putative benefits of higher feeding frequencies have been mentioned above.

There was enormous variation in diet composition, with diets that were based mainly on grass hay, diets based mainly on pelleted food, and diets based mainly on vegetables (Fig. 6). Out of 56 zoos, 45% (n=25) did not offer grass hay. The amount of dry matter provided in non-forage items averaged at 361 g, with a large range from 22 to 1010 g per animal (Table 2). In comparison to the assumed 450 g of dry matter intake per adult individual, 20% (n=11) of the zoos offered non-forage items in excess of that threshold, leading to the assumption that these animals would not have had to ingest any forages even if offered. This seems to be confirmed by noting that 8 of

Tab. 2: Total amount of non-forage (no hay, grass or branches) items offered in dry matter (DM) per animal and day, the estimated* DM intake of individual food categories incl. hay/grass and branches per animal and day (and the % of total assumed intake) in Indian (*Hystrix indica*) and African crested porcupines (*Hystrix cristata*) in 56 European zoos.

	Total non-forage	Vegetable	Fruit	Seeds Cereals	Nuts	Animal matter	other	Pellet	Hay Grass	Branches
	g DM (% of total assumed DM intake)									
Mean	322 (72%)	161 (36%)	40 (9%)	13 (3%)	10 (2%)	4 (1%)	1 (0%)	93 (21%)	93 (21%)	34 (8%)
SD	197	100	48	31	18	12	6	104	113	678
min	22	0	0	0	0	0	0	0	0	0
max	1020	433	216	159	79	73	34	366	428	283

*assuming a total daily dry matter intake of 450 g per adult animal (Hagen et al. 2019), and a complete ingestion of non-forage feeds offered; for details see methods

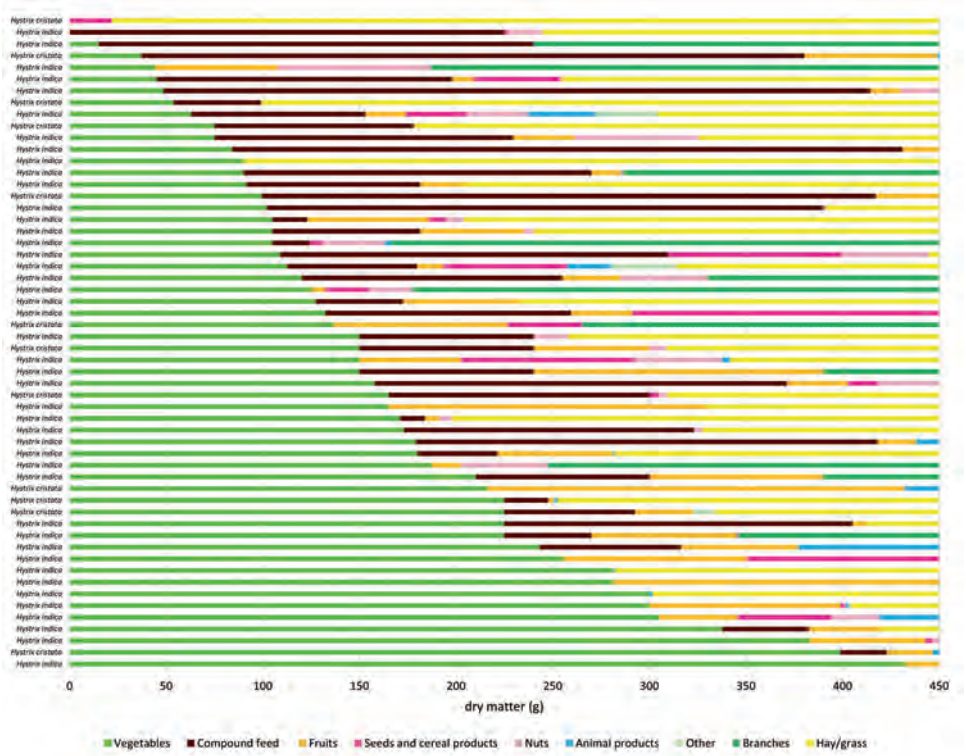

Fig. 6: Proportion (on a dry matter basis) of hay/grass, fruits, vegetables, compound feed, nuts, seeds and cereal products, animal products, branches and other foods in the diet of Indian crested porcupines (*Hystrix indica*) and African crested porcupines (*Hystrix cristata*) in European zoos.

these 11 zoos (73%) did not offer hay or grass to their porcupines. Of the remaining 45 zoos that fed non-forage items at amounts below that threshold, only 17 (38%) did not offer hay or grass. Zoos that did not offer grass or hay offered an average of 432 ±236 g DM (range 167-1020 g) of non-forage items per animal, whereas this was 304 ±140 g DM (range 22-678 g) of non-forage

items in zoos that offered grass or hay. Only 9 zoos (15%) did not offer gnawing material in the form of branches to their porcupines.

On average, vegetables represented the largest proportion of estimated dry matter intake, (and were used in 54 zoos) followed by compound feeds (pellets, in 39 zoos) and hay; in decreasing proportion, fruit (in 42 zoos), seeds/cereals (in 19 zoos), nuts (in 24 zoos), animal matter (in 24 zoos) and others represented much lower average proportions (Table 2). 72% of the zoos (n=42) fed one or several compound feed products to their porcupines; the products were of a huge variety, including products for rodents (n=16), dogs and cats (n=12), rabbits (n=9) and birds (n=2); there was no product that was used predominantly. The animal matter offered included deer antlers (n=10), other bones (n=15), eggs (n=7), cooked meat (n=5), day-old chicks (n=1). Minerals and supplements were given in 22% of zoos (n=13).

Some diets were traditional in the sense of Fens & Clauss (2024), as anthropomorphic diet items such as bread, grains and cultivated fruits are still fed quite often (as suggested for porcupines by Weir, 1967; Tohmé & Tohmé, 1980; van Aarde, 1985a; Puschmann, 2004, Hagen et al., 2019). So to speak, many zoos use the feeding habits of "pest" porcupines that feed on agricultural products as guidelines for their feeding regime, not the feeding habits of porcupines from unmodified habitats. This is in distinct contrast to current recommendations, which state explicitly that grass hay, grasses, vegetables and high-fibre pellets low in starch and soluble carbohydrates should be fed, and that warn against the use of cultivated fruit, grains and commercial dog and cat food (Yarto-Jaramillo, 2015). Fens & Clauss (2024) suggested that, in the face of existing recommendations, the fact that some zoos continue to use anthropomorphic diets may have cultural rather than biological reasons.

The data of the present study can be interpreted as a state of transition with respect to dietary regimes. The amount of cultivated fruit fed ranged from 0 to 216 g of dry matter per animal and day; eleven zoos explicitly reported that they do not feed any fruit to porcupines, but on the other hand, eleven zoos offered non-forage diet items at magnitudes above the assumed daily dry matter intake of porcupines. The proportion of zoos that did and did not include grass hay in the diet of their porcupines was nearly even (55% vs. 45%). Across all zoos, the amount of non-forage diet items appeared roughly balanced against the offer of forage items, suggesting that if forced to do so, porcupines do ingest, and use, forages; as a conclusion, we suggest that all zoos should adopt the recommendation to base their diets on high-quality grass hay as a staple forage, supplemented by fresh branches (a legal requirement in several countries), green leafy vegetables, only very limited amounts of cultivated tubers, and a high-fibre, mineralized pellet to ensure appropriate mineral coverage. For example, the feeding experiment of Hagen et al. (2019) showed that porcupines do ingest relevant amounts of a high-fibre, lucerne-based pellet – if no other diet items are available.

Three important consequences will ensue if forage-based, high-fibre diets are not used. First, porcupines on diets of higher nutrient density (i.e., lower fibre content) are less likely to practice coprophagy. Coprophagy is an evolved digestive adaptation of various mammal taxa, including lagomorphs, muroid rodents and hystricomorph rodents such as *Hystrix* spp., where the gut bacteria (a valuable protein source) are not excreted with the normal faeces but retained, by a separation mechanism in the colon, and excreted as 'soft faeces' that are ingested by the animal directly when excreted from the anus (reviewed in Clauss et al., 2023). Even though *Hystrix* spp. have the anatomical prerequisite for the colonic separation mechanism (Hagen et al., 2019), this behaviour has long been considered nonexistent in these species until confirmed visually very recently (Polotzek et al., 2023). Because coprophagy is a nutritional behaviour that is not expressed on nutrient-dense diets (Hagen et al., 2015; Guerra Aldrigui et al., 2018), the historical feeding practices still used in some of the investigated zoos may have contributed to the impression that porcupines do not practice coprophagy. This issue raises the general question how feeding practices in zoos can affect natural behaviours (e.g., Friedmann et al., 2023; Bähler et al., 2024).

Second, diets consisting of energy-dense items typically require less ingestion time until saturation is reached, even though voluntary intake of these items will often overshoot energetic requirements, as demonstrated in rabbits (Prebble et al., 2015a). Even though similar investigations in porcupines are lacking, it is plausible to assume that they would be active for larger parts of the day if fed diets higher in fibre and lower in energy density. Given the large variety in porcupine diets documented in the present study, comparative behavioural studies on the activity budgets of

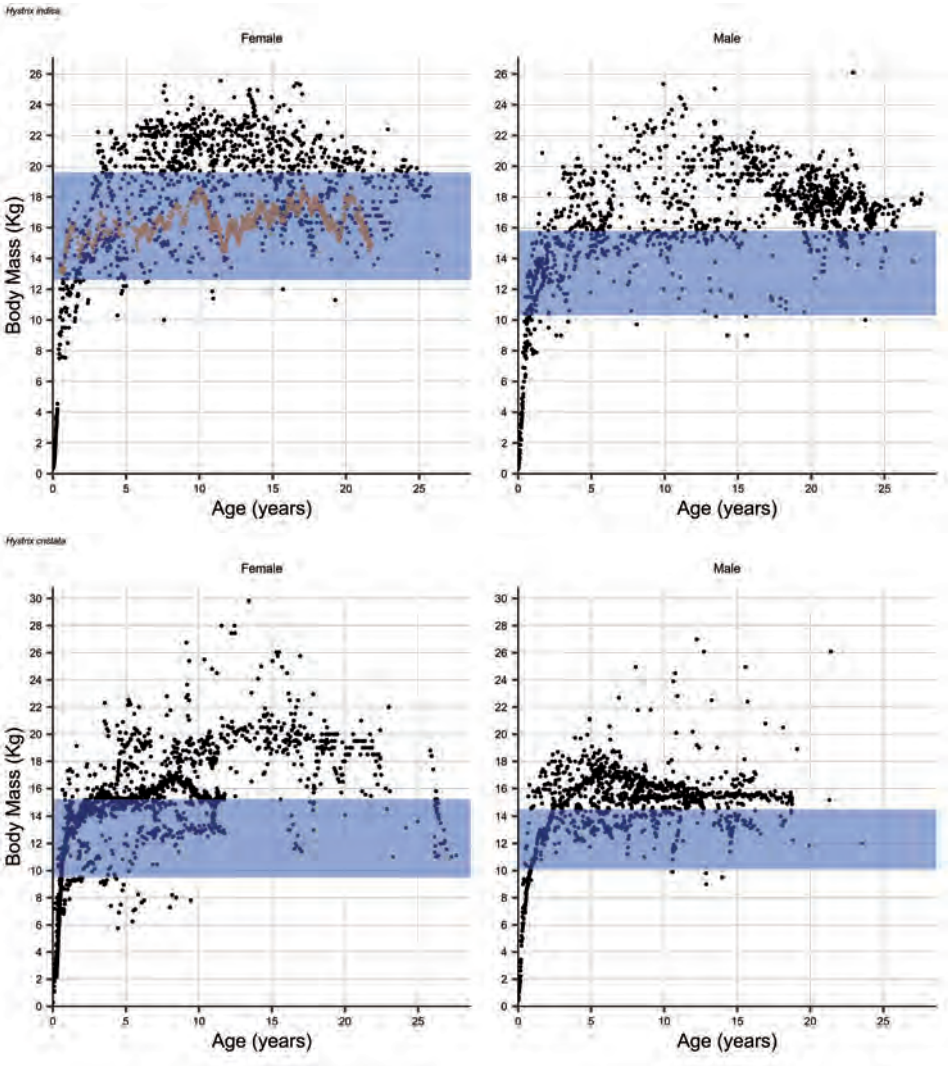

Fig. 7: Body mass in Indian crested porcupines (*Hystrix indica*; **A**) and African crested porcupines (*Hystrix cristata*; **B**) kept globally in zoos (black dots) compared to literature data for free-ranging specimens (blue bar; for details see table 5). Note that a large number of zoo individuals exceed the body mass range reported for free-ranging animals, and a fluctuating pattern suggestive of a seasonal pattern in a single *H. indica* female (orange dots)

Tabl. 3: Body mass records (in kg) for adult, free-ranging in Indian (*Hystrix indica*) and African crested porcupines (*Hystrix cristata*) in natural habitats.

Source	n	minimum	average	maximum
Hystrix indica				
			females	
(Girish et al. 2006)	2	14.5	14.9	15.3
(Alkon et al. 1986)	1	-	17.8	-
(Alkon 1984)	6	12.6	16.8	19.6
			males	
(Vishnugurubaran et al. 2021)	1	-	12.5	-
(Alkon 1984)	8	10.3	11.9	15.8
			unknown sex	
(Sever and Mendelssohn 1991)	10	-	13.9	-
(Alkon and Saltz 1988a)	11	-	14.1	-
Hystrix cristata				
			females	
(Pigozzi 1987a)	10	-	11.4	-
(Mori et al. 2015a)	30	-	11.6	-
(Mori et al. 2015a)	11	-	11.8	-
(Mori et al. 2015a)	4	9.5	11.8	14.0
(Mori et al. 2015a)	1	-	10.3	-
(Mori et al. 2015a)	1	-	14.5	-
(Angelici et al. 2009)	3	10	12.3	15
(Coppola et al. 2020d)	6	11.0	12.9	15.2
(Mori and Lovari 2014)	42	-	12.1	-
(Pigozzi 1987b)	9	-	11.1	-
(Sonnino 1998)	1	-	13.8	-
(Corsini et al. 1995)	1	-	13.8	-
			males	
(Pigozzi 1987a)	14	-	10.1	-
(Mori et al. 2015a)	20	-	12.4	-
(Mori et al. 2015a)	27	-	11.3	-
(Mori et al. 2015a)	2	10.5	11.8	13.0
(Coppola et al. 2020d)	5	11.0	12.6	14.5
(Mori and Lovari 2014)	40	-	11.4	-
(Pigozzi 1987b)	8	-	10.2	-
(Sonnino 1998)	3	-	12.3	-
(Corsini et al. 1995)	3	11.5	12.4	13.5
			unknown sex	
(Santini 1980)	n.g.	-	15	20

n.g. not given

porcupines under different feeding regimes would be highly feasible, including observations on the frequency of coprophagy.

Tab. 4: Body mass records (in kg) for adult Indian crested porcupines (*Hystrix indica*) and African crested porcupines (*Hystrix cristata*) under human care.

Source	n	minimum	average	maximum
Hystrix indica				
			females	
(Stalder et al. 2012)	10	9.5	11.3	13.1
this study	89	10.0	17.4 ±3.1[A]	24.8
this study	89	10.0	17.4 ±3.1[A]	24.8
			males	
(Švara et al. 2015)	1	-	14.5	-
(Stalder et al. 2012)	10	11.0	11.8	12.6
(Alkon et al. 1986)	4	14.7	16.1	18.1
this study	97	9.0	15.8 ±3.3[B]	24.2
			unknown sex	
(Hagen et al. 2019)	3	13.1	16.1	18.1
Hystrix cristata				
			females	
this study	94	8.4	17.3 ±3.6[a]	25.3
			males	
this study	54	9.4	16.1 ±3.3[b]	26.5

A,B difference significant at p = 0.001
a,b difference tends towards significance at p = 0.066

Third, because voluntary intake of diet items that are highly palatable due to their energy density (e.g., the content of sugar or starch) will likely be higher than energetic requirements, higher growth rates and obesity are logical consequences of such diets (Prebble et al., 2015b, Głogowski et al., 2018). In their natural habitat, *H. indica* body mass averages at 16.5 kg for females and 12.0 kg for males, and that of *H. cristata* at 11.9 kg for females and 11.4 kg for males (Tab. 3). Body mass data published previously for *H. indica* under human care were within the range of free-ranging specimens (Tab. 4). However, the average body mass of the global zoo data for *H. indica* was 17.4 ±3.1 kg for females and 15.8 ±3.3 kg for males. For *H. cristata*, this was 17.3 ±3.6 kg for females and 16.1 ±3.3 kg for males. Thus, zoo animals often surpassed the body mass range reported for free-ranging specimens (Fig. 7); even though the body mass data are not directly linked to the individuals surveyed in the present study, these data thus support the suspicion that many of the diets reported in our survey might trigger obesity.

Hystrix spp. are adapted to a seasonal accretion of adipose tissue reserves that will contribute to surviving through the wintertime (Alkon et al., 1986). It has been suggested that species that evolved a seasonal metabolism including the build-up of adipose tissue stores are particularly susceptible to obesity in managed care (Mellor et al., 2020), which would mean that body mass management is important in porcupines. A single female *H. indica* showed a clear, life-long pattern of seasonal fluctuation (Fig. 7). Whether this pattern occurs more frequently in zoos was difficult to assess within the present dataset; in particular, it has been suggested that seasonal body mass fluctuations might only be evident in animals that are not obese (Gerstner et al., 2016). Given the ease with which porcupines can reportedly be trained, and the availability of platform scales onto which the animals could be easily guided using a target, it would be highly interesting in the future to document body mass across several seasons in porcupines that are not obese, and to directly

compare the body masses of porcupines in zoos under different feeding regimes. Additional, more data on free-ranging specimens would be welcome.

With respect to sexual size dimorphism, zoo data suggests a highly significant female-biased sexual size dimorphism for *H. indica* (Tab. 4) that corresponds to reports in the literature (Tohmé & Tohmeé, 1980; Alkon & Saltz, 1985). By contrast, the numerical difference between the sexes in *H. cristata* only tended towards significance in the zoo data (Tab. 4), similar to the criticism voiced by Mori & Lovari (2014) on the previous suggestion of Pigozzi (1987a) that this species also has a female-biased sexual size dimorphism.

The actual dietary requirements of porcupines are largely unknown. *Hystrix* spp. have been suggested to require UV-light induced vitamin D for a normal calcium metabolism, and this assumption has been used as an explanation for diurnal sunbathing behaviour in these generally nocturnal species (Coppola et al. 2019). However, the urine of a *Hystrix* ssp. was found to contain high levels of calcium (Haim et al. 1992b), suggesting that the calcium metabolism of these species is similar to that of lagomorphs and other hystricomorph rodents in that more calcium is absorbed from the digestive tract than necessary, and the surplus excreted in the urine (Hagen et al. 2015). It has been suggested that in such species, vitamin D may be of little relevance for calcium metabolism (Liesegang et al. 2024).

While 41% (n=24) of the zoos surveyed also feed animal products to porcupines, 59% (n=35) did not do so. The question of whether animal material should be fed to porcupines is also answered differently in legal requirements. Whereas the feeding of animal matter is not regulated in Germany and Switzerland, porcupines must receive bones with meat residues in Austria (Table 1). This discrepancy is also reflected in the scientific literature on the natural diets of crested porcupines: Table 5 summarises which publications have described their diets as containing or not containing bones, insects, flesh and hairs of animals. Because collecting and ingesting bones has been shown in both species (Duthie and Skinner 1986; Kadhim 1997; Kiibj 2009; O'Regan et al. 2011; Coppola et al. 2020c), it can be assumed that porcupines in the wild eat animal products when they are available. While this need not translate into a requirement of daily offerings of bones, the occasional provision of bones can likely be considered an imitation of the natural diet that can be used to structure the life of zoo porcupines beyond a daily rhythm.

Tab. 5: Overview of the animal components of the diet of free-ranging Indian (*Hystrix indica*) and African (*Hystrix cristata*) crested porcupines.

Author	Species	Animal product	Comments
Mori et al. (2021)	*H. cristata*	Insects	Only in February-March (during lactation)
Coppola et al. (2020c)	*H. cristata*	Meat	Scavenging behaviour recorded
Coppola and Felicioli (2021)	*H. cristata*	Bones	During reproduction
Kiibj (2009)	*H. cristata*	Bones	
Kaur et al. (2019)	*H.* spp.	Bones	
Akram et al. (2017)	*H. indica*	Bones, hairs of animals	5.6 – 6.4 % of the ratio, whole year round
Kadhim (1997)	*H. indica*	Insects, bones	
Bounaceur et al. (2024)	*H. cristata*	No animal matter	
Mori et al. (2017)	*H. cristata*	No animal matter	
Hafeez et al. (2011)	*H. indica*	No animal matter	
Khan et al. (2021)	*H. indica*	No animal matter	

Finally, the participating zoos did not use a variety of feeding methods to offer diet items to their porcupines. Given that porcupines often dig out their food in natural habitats (Shachak et al. 1991; Bragg et al. 2005), methods of feeding them in a way that they have to dig out diet items, e.g. in a larger area of relatively loose sand so that food is easy to hide, might be an interesting method of

using a natural behaviour. Again, behavioural studies on porcupines under a variety of methods of offering the same diet items would be a promising future study.

Conclusions

The variety of husbandry and feeding practices noted in our survey reflects the fact that no husbandry guidelines exist for these species. The typical limitations of a survey based on a questionnaire apply. Even though a large amount of data can be gathered in this way, very few conclusions about the effect of one parameter on another can be made. Hence, this study mainly serves as a status quo baseline that may be useful in the future to assess changes or progress in porcupine husbandry.

Indian and African crested porcupines are relatively easy to keep, and they rarely suffer from serious clinical diseases based on current observations under human care. Care must be taken with group composition to avoid intraspecific aggression. Since they are also familiar with temperatures around freezing in their natural habitat, they can easily have access to outdoor enclosures all year round in Central Europe. However, due to the animals' distinct ability to escape, these enclosures must be well protected against digging under, climbing over or biting through the fence. Following the natural diet of porcupines, their diet in human care should also consist largely of browse and branches, hay, grass and vegetables as well as high-fibre pellets. Animal products such as bones should also be provided on occasion. Due to their tendency to become obese, cultivated fruit, grain products and low-fibre pellets should not be used in human care, and cultivated tubers – although seemingly corresponding to the natural diet of tubers and roots – are also most likely higher in easily digestible carbohydrates than their uncultivated counterparts and should therefore not be used. Changes in routines, such as feeding in several small portions and at different locations or hiding the food, or destroying burrow structures at larger time intervals to stimulate digging, might improve health and well-being. Improvements in historical zoo survivorship likely indicate more engaged husbandry over time; this could be continued by producing husbandry guidelines for these species.

Acknowledgments

We thank the participating zoos for supporting this study. This research was made possible by the worldwide information network of zoos and aquariums which are members of Species360, and is authorized by Species360 Research Data Agreements # 2019-Q3-RR3 and # 84212. There is no funding to report.

Competing interests

The authors have no conflicts of interest.

Zusammenfassung

Indische Weißschwanzstachelschweine (*Hystrix indica*) und Gewöhnliche Stachelschweine (*Hystrix cristata*) sind beliebte Zootiere in Europa und werden insgesamt in rund 400 Einrichtungen gehalten. Ziel dieser Studie war es, die Haltungs- und Fütterungsbedin-

gungen dieser beiden Stachelschweinarten in europäischen Zoos genauer zu untersuchen und häufige Krankheitsbilder zu erfassen. Zu diesem Zweck wurden Daten von 90 Zoos erhoben, die an der Studie teilnahmen. Im Durchschnitt wurden 3,8 ±2,7 Stachelschweine pro Gehege gehalten, wobei die meisten Zoos (70 %) über ein kombiniertes Außen- und Innengehege verfügten. Die durchschnittliche Größe des Außengeheges betrug 164 ±196 m² und wurde durch ein durchschnittliches Innengehege von 14 ±18 m² ergänzt. Die gängigsten Methoden zur Populationskontrolle waren gleichgeschlechtliche Gruppen (39 %) und ein „Breed and Feed"-Regime (28 %). Nur 23 % der Zoos praktizierten ein medizinisches Training mit ihren Stachelschweinen. Obwohl Stachelschweine in menschlicher Obhut selten erkranken, gibt es einige typische Krankheitsbilder: 22 % (n = 10) aller klinischen Fälle in dieser Studie betrafen die Haut, wobei die Hälfte dieser Hauterkrankungen durch innerartliche Aggressionen verursacht wurde. Wahrscheinlich aufgrund der verbesserten Haltungsbedingungen in den letzten Jahren und der Fortschritte in der Zootiermedizin zeigte die gesamte europäische Zoopopulation beider Arten eine Verbesserung der historischen Überlebensrate in Zoos sowohl für adulte als auch für juveline Tiere. Die durchschnittliche geschätzte Futterration der Stachelschweine bestand aus Gemüse, pelletiertem Kraftfutter, kultivierten Früchten (Obst), Samen und Getreideprodukten, Nüssen, tierischen Produkten und einer geschätzten Aufnahme von etwa 90 g Trockenmasse Heu oder Gras. Bei der Fütterung von Obst, pelletiertem Kraftfutter, Heu und tierischen Produkten gab es enorme Unterschiede: Elf Zoos fütterten ausdrücklich kein Obst, während in den übrigen Zoos der Anteil an Obst an der Gesamtration zwischen 0,7 und 48 % der gesamten Trockenmasse lag. Nur 56 % (n = 33) aller befragten Zoos fütterten ihren Stachelschweinen Heu, und in diesen Zoos war die durchschnittliche Menge an Nicht-Raufutter geringer, was darauf hindeutet, dass die Aufnahme von Heu mit einem geringeren Angebot anderer Futtermittel bewirkt werden kann. 20 % (n=11) der Zoos boten Nicht-Raufutter in Mengen an, die über der geschätzten Tagesaufnahme lagen, was zu der Annahme führt, dass ihre Tiere selbst bei Angebot kein Raufutter aufgenommen hätten. Die durchschnittliche Körpermasse von in Zoos gehaltenen *Hystrix* spp. war höher als die von freilebenden Exemplaren, was auf eine energiereiche, raufutterarme Ernährung in Zoos zurückzuführen sein könnte, die zu Fettleibigkeit führt. Daher sollten kein Obst, Getreideprodukte oder faserarme Pellets verwendet werden. Wir empfehlen, die Ernährung auf hochwertiges Grasheu als Grundfutter zu stützen und dieses durch frische Zweige, grünes Blattgemüse, begrenzte Mengen an angebauten Knollenfrüchten und mineralhaltige Pellets mit hohem Fasergehalt zu ergänzen, um eine angemessene Mineralstoffversorgung sicherzustellen. Zusammen mit unserer umfangreichen Literaturrecherche können die Ergebnisse dieser Studie als Grundlage für Haltungsrichtlinien für diese Arten dienen.

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Appendix I

Questionaire (which was spread via surveymonkey)

1. Introduction

This survey was designed by Martin Polotzek (zoo director and veterinarian in Zoo Cleves, Germany ["Tiergarten Kleve"]) and Marcus Clauss (Vetsuisse University, Zurich) to create a comprehensive overview of husbandry conditions of Indian crested porcupines (*Hystrix indica*) and African crested porcupines (*Hystrix cristata*) in European zoos. Furthermore, the information obtained should be used to make best practice guidelines for husbandry, feeding and veterinary treatment.

2. About your Indian crested porcupines

Name and location of your zoo:
On 31st December 2021 how many Indian crested porcupines lived in your institution?
_____ , _____ , _____ (male, female, unknown)
Please give us an overview about your group structure and write the number of your animals in the following datasheet. Alternatively, you can send us your Indian crested porcupine-taxon report from ZIMS to polotzek@tiergarten-kleve.de.

Breeding animals	
Adults (>2 years; excl. breeding pair)	
Subadults (between 1 and 2 years)	
Juveniles (< 1 year)	

Are your Indian crested porcupines socialized with other animal species?
No
Yes, with: _____
If they are socialized with other species, do you see a negative aspect for one of the species?
No
Yes, if yes, please specify:
Do you have any veterinary problems resulting from association with other species?
No
Yes, following veterinary problems:
Why do you keep Indian crested porcupines? (Multiple selection possible)
Education
Research
High visitor attractivity
Easy to keep
To revive a vacant enclosure
Low acquisition and maintenance costs
Other, please specify:

3. Enclosure

In which type of housing are your Indian crested porcupines kept?
Only indoor enclosure
Indoor and outdoor enclosure
Only outdoor enclosure without heated boxes
Only outdoor enclosure with heated boxes
To get an overview about your Indian crested porcupine enclosure, please give us the following information for the **outdoor** enclosure:
Seize:
Barrier height (at the lowest point):
Underground protection:
Ground:
Structure elements:
Which type of barriers are you using for your Indian crested porcupine enclosure: (Multiple selection possible)
Wire mesh
Glass
Cement wall
Wood wall
Electric fence
Trenches
Other: _____
To get an overview about your Indian crested porcupine enclosure, please give us the following information for the **indoor** enclosure:
Seize:
Temperature:
Separation possibility:
Ground/bedding:
Structure elements:
Did you have any breakout events in your porcupine enclosure? If yes, please specify?

4. Keeping

Which kind of contact do you practice with your Indian crested porcupines?
Direct contact (keepers and other staff members are at the same time in the same enclosure as the porcupines)
Indirect contact (the enclosure is entered only when the porcupines are locked away)
Do you practice medical training in Indian crested porcupines? (YES / NO)
If yes, which exercise(s) do you use? (Multiple selection possible)
Target training
Ultrasound training
Blood sample training
Mouth examination training
Other - please specify:
How do you catch your Indian crested porcupines? (Multiple selection possible)
Net
Drift board
Catch cage

Distance immobilization (blow pipe…)
Other – please specify:
Are there any special events with your Indian crested porcupines? (Multiple selection possible)
Behind-the-scenes tours
Meet the public
Public feeding/keepers talk
Other, please specify:
There is no special event with our porcupines.
Did you have any human injuries due to porcupine interaction? (YES / NO; if yes, please specify)

5. Nutrition

Please, send us your feeding instruction for Indian crested porcupines via email: polotzek@tiergarten-kleve.de.
Do you have any personal comments regarding Indian crested porcupine feeding that you want to share?

6. Veterinary medicine

Please, send us your Indian crested porcupine veterinary reports from the last 10 years to polotzek@tiergarten-kleve.de.
Do you use reproductive management other than placing offspring to other facilities in your Indian crested porcupines?
Chemical contraception (please, specify)
Breed and cull
Same-sex-groups
We don't use any of these management options in our porcupines.
Do you have personal experiences or opinions you want to share on
Vaccination
Parasites and antiparasitic treatment
Specific diseases
Antibiotic treatment
Anesthesia and analgesia

7. Pathological findings

Please, send us your Indian crested porcupine pathological reports from the last 10 years to polotzek@tiergarten-kleve.de.
Do you have any personal comments regarding Indian crested porcupine pathology that you want to share?

Additional questions about nutrition which were send separately via email:
Do you feed pellets to your porcupines? If yes, which kind of feed pellets?
Do you feed hay to your porcupines?
Do you feed branches to your porcupines?
Do you feed animal products like bones or meat to your porcupines?

Appendix II

Drugs used in Indian crested porcupines (*Hystrix indica*) and African crested porcupine (*Hystrix cristata*). Information derived from ZIMS in italics

Drug name	Drug dose	Comments
Antimicrobials and Antifungals		
Amoxicillin	200 mg/animal SID IM	Pneumonia
Amoxicillin/clavulanic acid	140 mg/animal amoxicillin + 35 mg/animal clavulanic acid SID IM	Bronchopneumonia
Azithromycin	*10 mg/kg SID PO [1]*	
Cefalexin	*0.13-20 mg/kg BID PO [2]*	
Cefquinom		Topically in flushed abscess
Ceftrioxone	125 mg/animal SID IM x5d [19]	After abscess splitting
Doxycycline	*3-5 mg/kg BID PO [3]*	
Enrofloxacin	5-10 mg/kg SID IM or PO	
	5.5 mg/kg BID PO or 6.5 mg/kg SID PO [4]	
	6.4 mg/kg SID SC [4]	
	5.65 mg/kg BID PO[29]	
Marbofloxacin	0.38-2 mg/kg SID PO	
	2.5 mg/kg SID PO [5]	
Metronidazole	*19 mg/kg BID PO [6]*	
Streptomycin + penicilin	200,000 IE/animal penicillin + 200,000 IE/animal streptomicin SID SC	
Trimetoprim-Sulfodiazin	12-40 mg/kg BID PO	Skin conditions

Drug name	Drug dose	Comments
Anaesthesia		
Ketamine + medetomidine	3.8 mg/kg (K) + 0.06 mg/kg (M)	Antagonize with 0.3 mg/kg atipamezol
	4 mg/kg (K) + 0.046 mg/kg (M) [20]	*Abnormal recovery in 3.17 %*
	4.21 mg/kg (K) + 0.084 mg/kg (M) [30]	Shorter and calmer recovery compared to a combination of tiletamine-zolazepam with medetomidine
	6-10 mg/kg (K) + 0.01 mg/kg (M) [31]	
	3-4 mg/kg (K) + 0.03-0.04 mg/kg (M) [36, 37]	
Ketamine + xylazine	10.1 mg/kg (K) + 1.5 mg/kg (X)	Antagonize with 0.22 mg/kg atipamezol or 0.4 mg/kg yohimbine
	11.73 mg/kg (K) + 1.64 mg/kg (X) [21]	*Abnormal recovery in 3.45 %*
	15 mg/kg (K) + 1 mg/kg (X) [26; 27]	
	10 mg/kg (K) + 2 mg/kg (X) [33, 35]	
	5-10 mg/kg (K) + 1-2 mg/kg (X) IM [36, 37]	
	300 mg (K) + 20 mg (X) IM per adult animal [38]	
Butorphanol + ketamine + medetomidine	*0.3 mg/kg (B) + 4.18 mg/kg (K) + 0.06 mg/kg (M) [22]*	*Abnormal recovery in 4.17 %*
Dexmedetomidine + ketamine	*0.027 mg/kg (D) + 5.49 mg/kg (K) [23]*	
Ketamine + midazolam	3-4 mg/kg (K) + 0.03-0.04 mg/kg (M) IM, IV [37]	
Ketamine + acepromazine + hylase	5.5 mg/kg (K) + 0.25 mg/kg (A) + 7.5 IE/kg (H)	

Tiletamine-zolazepam	*8.86 mg/kg [24]*	*Abnormal recovery in 33.33 %*
	8.0 mg/kg [25]	
	4-8 mg/kg [32]	
	7.25 mg/kg [34]	
	4-6 mg/kg [36, 37]	
Tiletamine-zolazepam + medetomidine	3.7 mg/kg (TZ) + 0.0047 mg/kg (M) [30]	Longer and more restless recovery compared to a combination of tiletamine-zolazepam with medetomidine
Propofol	6-8 mg/kg IV [36, 37]	

Drug name	**Drug dose**	**Comments**
Sedatives and Tranquillizers		
Acepromazine	0.1 mg/kg IM [36, 37]	
Diazepam	0.1-1.0 mg/kg IM, IP, PO [36, 37]	Unpredictable results and irritations during IM administration
Midazolam	0.1-0.5 mg/kg IM [36, 37]	Premedication with lower doses
Xylazine	1-5 mg/kg IM, SC [36, 37]	

Drug name	**Drug dose**	**Comments**
Analgesic		
Buprenorphin	*0.01-0.6 mg/kg SC once [7]*	
	0.01-0.03 mg/kg IM, SC q8-12 h [36, 37]	
Butorphanol	0.5 mg/kg IM, SC q4h [36, 37]	
Carprofen	4 mg/kg SID PO	
	1.8-4.4 mg/kg SID PO [8]	

Flunixin	0.5 mg/kg IM, SC SID-BID [36, 37]	
Gabapentin	15 mg/kg BID	
	5 mg/kg SID PO or 9 mg/kg BID PO [9]	
Ketoprofen	1-3 mg/kg IM, SC SID [36, 37]	
Meloxicam	0.2-1.25 SID PO or SC or IM	
	0.5 mg/kg SID PO [10]	
	0.4 mg/kg SID IM [10]	
	0.2 mg/kg SID PO [28]	
	0.1-0.3 mg/kg SC, PO SID-BID [36, 37]	
Metamizol	37.5 mg/kg	
Morphine	1-3 mg/kg IM, SC q4-6h [36, 37]	Usually used as a single dose before surgery
Oxymorphone	0.1 mg/kg IM, SC q6-12h [36]	
Piroxicam	*0.4 mg/kg SID PO [11]*	
Prednisolon	0.2 mg/kg SID PO	
Tramadol	*6.6 mg/kg BID PO [12]*	
	0.5-5 mg/kg SID-BID PO [36]	

Drug name	**Drug dose**	**Comments**
Antiparasitic		
Fenbendazole	10 mg/kg SID PO x3d	
	21 mg/kg SID PO x5d [13]	
Ivermectin	0,2-1.5 mg/kg SC or PO once	
	0.4 mg/kg PO three time q7d	
	0.2 mg/kg SC or PO once [14]	

Selamectin	120 mg/animal topically	
Drug name	**Drug dose**	**Comments**
Other		
Arnica montana Dil. C 30	2 ml/animal	After chemical castration
Atropine	0.03 mg/kg SC, IM [36, 37]	
Doxapram	*0.5-6 mg/kg IM [15]*	
Furosemide	*2.4 mg/kg SID PO [16]*	
Glycopyrrolate	0.01 mg/kg IM, SC [36, 37]	
Pentobarbital	*90-400 mg/kg intracardiac [17]*	Euthanasia
Pimobendan	*0.23 mg/kg BID PO [18]*	
Vitamin E-Selen	10 mg/juvenile animal vitamin E + 0,07 mg/juvenile animal selen SC	Young animal prophylaxis on day 4

Diagnosed bacteria by the participating zoos	**Diagnosed fungi by the participating zoos**	**Diagnosed parasites by the participating zoos**
Acinetobacter dijkshoorniae	*Aspergillus fumigatus*	*Trichuris* sp.
Bordetella bronchiseptica		*Strongylidae*
Clostridium sordelli		*Giardia*
Clostridum perfringens		
Lactobacillus sp.		
Lecleria adecarboxylata		
Pseudomonas sp.		
Psychrobacter sp.		
Raoultella sp.		
Streptococcus canis		
Streptococcus sp.		
Vibrio metschnikovii		

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[3]: ZIMS Drug Usage Extracts for *Hystrix indica* and Doxycycline. (2022, September 06). Species360 Zoological Information Management System. Retrieved from http://zims.Species360.org. filters: Hystrix indica/Indian crested porcupine
[4]: ZIMS Drug Usage Extracts for *Hystrix indica* and Enrofloxacin. (2022, September 06). Species360 Zoological Information Management System. Retrieved from http://zims.Species360.org. filters: Hystrix indica/Indian crested porcupine
[5]: ZIMS Drug Usage Extracts for *Hystrix indica* and Marbofloxacin. (2022, September 06). Species360 Zoological Information Management System. Retrieved from http://zims.Species360.org. filters: Hystrix indica/Indian crested porcupine
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[14]: ZIMS Drug Usage Extracts for *Hystrix indica* and Ivermectin. (2022, September 06). Species360 Zoological Information Management System. Retrieved from http://zims.Species360.org. filters: Hystrix indica/Indian crested porcupine
[15]: ZIMS Drug Usage Extracts for *Hystrix indica* and Doxapram. (2022, September 06). Species360 Zoological Information Management System. Retrieved from http://zims.Species360.org. filters: Hystrix indica/Indian crested porcupine
[16]: ZIMS Drug Usage Extracts for *Hystrix indica* and Fursosemide. (2022, September 06). Species360 Zoological Information Management System. Retrieved from http://zims.Species360.org. filters: Hystrix indica/Indian crested porcupine

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[21]: ZIMS Drug Usage Extracts for *Hystrix indica* and ketamine + xylazine. (2022, September 06). Species360 Zoological Information Management System. Retrieved from http://zims.Species360.org.
filters: Hystrix indica/Indian crested porcupine
[22]: ZIMS Drug Usage Extracts for *Hystrix indica* and butorphanol + ketamine + medetomidine. (2022, September 06). Species360 Zoological Information Management System. Retrieved from http://zims.Species360.org.
filters: Hystrix indica/Indian crested porcupine
[23]: ZIMS Drug Usage Extracts for *Hystrix indica* and dexmedetomidine + ketamine. (2022, September 06). Species360 Zoological Information Management System. Retrieved from http://zims.Species360.org.
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Appendix III

Infectious agents diagnosed in Indian crested porcupines (*Hystrix indica*) and African crested porcupines (*Hystrix cristata*) by the participating zoos

Diagnosed bacteria by the participating zoos	**Diagnosed fungi by the participating zoos**	**Diagnosed parasites by the participating zoos**
Acinetobacter dijkshoorniae	*Aspergillus fumigatus*	*Trichuris* sp.
Bordetella bronchiseptica		*Strongylidae*
Clostridium sordelli		*Giardia*
Clostridum perfringens		
Lactobacillus sp.		
Lecleria adecarboxylata		
Pseudomonas sp.		
Psychrobacter sp.		
Raoultella sp.		
Streptococcus canis		
Streptococcus sp.		
Vibrio metschnikovii		

DER ZOOLOGISCHE GARTEN
THE ZOOLOGICAL GARDEN

doi:10.53188/zg0046 Zool. Garten N.F. 93 (2025) 179-191

Breeding the Yellow-rumped Cacique (*Cacicus cela*) at Cologne Zoo

Zucht der Gelbbürzelkassike (*Cacicus cela*) im Kölner Zoo

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Abstract

The article describes and analyses the breeding of the yellow-rumped cacique (*Cacicus cela*) at Cologne Zoo, Germany. The holding conditions, husbandry, techniques to increase the breeding success and survival of young of this attractive icterid (New World blackbird) in a newly built tropical hall with associated enclosures are detailed. Between March 2021 and September 2025 19 breeding attempts led to 12 surviving offspring, all from a single pair, despite starting with four females and later trying with a second female in alternation. Disturbance and depredation, but also unfertilized eggs and accidents of the fledglings led the team towards moving the whole nest, once the hatchlings were mostly feathered, to a separation enclosure for more security and peace for the female and her nestlings. Up to four nests with either eggs or chicks were recorded per year in the period between late February to September, most of which disappeared. Breeding data reported from the wild for yellow-rumped caciques was mostly confirmed for breeding at Cologne Zoo, with nest building taking 12 days, clutch size between 2-3 eggs with laying up to 4 days apart, incubation likely lasted 13 days (12-16 days), fledging was with 25-26 days.

Keywords: Breeding, yellow-rumped cacique, *Cacicus cela*, Cologne Zoo

1. Introduction

The yellow-rumped cacique (*Cacius cela*) is a South American songbird of the Icteriidae family (Jaramillo & Burke, 1999; Fraga, 2011) (Fig.1). Icterids form a species-rich and diverse family within the order of passerines and are widespread in North, Central, and South America. The yellow-rumped cacique is found in evergreen lowland forests from Central Panama, Trinidad through northern South America south to Peru, Bolivia, and central Brazil (Corwin 2020).

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Fig. 1: Courting breeding male yellow-rumped cacique at Cologne Zoo. Photo: T. Breuer

Three subspecies are currently recognized, the nominate (*C.c.cela*) is found in northern South America, east of the Andes, *C.c. vitellinus* in southern Central America, and *C.c. flavicrissus* in the coastal lowlands west of the Andes from Ecuador to Peru. The subspecies kept at Cologne Zoo is the nominate and our birds originate from Suriname. As a species Yellow-rumped caciques are not classified as threatened. Males have a head-rump length of 28 (27 – 29) cm and weigh on average 109 g, while the much smaller females have a head-rump length of 23 (22 – 26) cm and weigh on average 71 g (Fraga, 2011). The birds are slender, predominantly black in color, with blue irises and a pale yellow beak. The rump, a large wing mirror, the cloacal region, and the small wing coverts are bright yellow in color. The female differs from the male not only in size but also in its slightly paler plumage. The male is a good singer and is constantly vocal during the breeding season.

The yellow-rumped cacique is very social, breeding in colonies that can range from 2-250 nests. Males are highly territorial and polygynous (Corwin 2020). Females build an enclosed, pouch-like, hanging nest that typically is placed near Polistine wasp nests high up in large trees. This provides protection from mammalian predators and botflies infestation of the nestlings. Male dominance via strict social hierarchy is determined by size and counter-singing. Only the highest-ranking males are allowed to reproduce. However, defending the females against rivals is so energy-intensive that the males often lose a lot of weight and are then displaced by stronger competitors. Lower-ranking males are pushed to the margins and protect the colony from nest predators such as the toco toucan (*Ramphastos toco*) and snakes, including the red-tailed boa (*Boa c. constrictor*), and the common tree boa (*Corallus hortulanus*), etc. There is also a distinct hierarchy among the females. Only experienced females succeed in acquiring good nesting sites. Only the females incubate the 2 to 3 eggs per clutch, from which the young hatch after about 13 to 14 days. The nestling period lasts about 25 days. Song dialects are specific to individual colonies of yellow-rumped cacique. The male does not contribute to nest

construction, incubation, or provisioning of the nestlings (Corwin 2020)

This article serves to describe our experience in breeding the species in a medium-sized free flying hall (Fig. 2) over a four-year period between May 2011 and September 2025, and the attempts to improve on the raising of young caciques, despite a high predation pressure by co-habiting species and chances for accidents. It largely drawns on an earlier publication (Breuer & Kiesow 2024) in German language, but has been expanded for another breeding year and with further details.

Fig. 2: View into the Arnulf and Elizabeth Reichert House from the visitor boardwalk level. In the foreground one of several palms (*Washingtonia* sp.) which are used by the cacique females for besting-building fiber collection. On the right side the adjacent separation enclosures can be seen. Photo: A. Sliwa

2. Husbandry, methods and results

Feeding at Cologne Zoo

The yellow-rumped cacique at Cologne Zoo are fed a mixed, finely chopped "fruit salad", consisting mainly of blueberries, which are frozen at harvest time and are very popular with all our fruit-eaters. They are also given a high quality soft insect food ("Insect Patee Premium" from Versele Laga®).

All soft-food eaters are fed twice a day (Pagel & Marcordes, 2011). During the rearing of young, the number of daily feedings is increased. Since the birds cannot hunt insects in their natural habitat to feed to their young, live insects (black beetle larvae (*Zophobas morio*), mealworm larvae (*Tenebrio molitor*), black soldier fly larvae (*Hermetia illucens*), large and small crickets (*Acheta domesticus*), etc.) are also available at all times in a Makrolon® (transparent

polycarbonate) tray during the rearing period. In general, mealworm larvae and black beetle larvae are not fed in the first few days, as the chitinous shell of the insects is very difficult to digest for the hatchlings during the first week of the nestling period. Thawed previously frozen insects, as well as "pinkies" (maggots of the small green fly (*Lucilia sericata*)), etc., offer variety and enrich the diet additionally. Fruits are also skewered and hung up in halves from time to time. This allows the birds to pick the food out of the fruit skins themselves as enrichment.

Enclosure/Keeping history at Cologne Zoo

Before the birds could move from their previous enclosures in the pheasantry to the renovated South America House (called Arnulf-and-Elizabeth-Reichert-House (AERH) for its main sponsors), all animals had to undergo a quarantine period, the length of which varied depending on the species. The move to the new 400 m² and up to 12 m high home took place in May 2021, an immersion exhibit with animals and plants from Central and South America (Fig. 2). The visitors can here experience the rain forest of tropical America with a small subset of its flora and fauna, where they can walk through on a raised boardwalk. While yellow-rumped cacique were kept in the pheasantry at Cologne Zoo since March 2000 and have been bred there since June 2003 in smaller indoor and outdoor aviaries, a second breeding group of yellow-rumped caciques was established in the AERH. The birds share this tropical freeflight with various other species such as Brazilian tanagers (*Rhamphocelus bresilia*), green tanagers (*Gubernatrix cristata*), red cardinals (*Cardinalis cardinalis*), short-crested pigeons (*Geotrygon versicolor*), Socorro doves (*Zenaida graysoni)*, cinnamon tinamous (*Tinamus solitarius*), Tataupa tinamous (*Crypturellus tataupa*), sunbitterns (*Eurypga helias*), two-toed sloths (*Choloepus didactylus*) and two monkey species, white-faced sakis (*Pithecia pithecia*) and golden lion tamarins (*Leontopithecus rosalia*). Guira cuckoos (*Guira guira*) are also housed there during the colder months as winter quarters. The hall is constantly heated to 23°C during the colder part of the year, and the house warms up further depending on the amount of sunlight received over the spring, summer to autumn months. When over 28°C the central air-conditioning system is activated for cooling. The average humidity is 70–90%. The relatively constant temperature and humidity in the house influence the breeding, which begins in the spring and lasts until autumn. The climate also promotes plant growth. An adjacent outdoor aviary (29 m², 3 m high), directly connected to the hall via slide openings on the visitors' side of the house, is popular with the birds. Only in the event of severe frost the animals' access to this outdoor enclosure is restricted and they make use of it regularly, particularly during warmer weather. Adjacent to the main free-flying hall, still within the house, there are 7 separation aviaries with 12 mm mesh, 6 of them with each 3 x 2.5 m (7.5 m² surface) and 3 m high, connected through sliding doors with each other. Each separation aviary also has one guillotine slide opening to the main hall for management of climbing and flying animals.

Breeding at Cologne Zoo/Breeding protocol

For a complete view, yellow-rumped caciques were kept in the pheasantry at Cologne Zoo since March 2000 and have bred there since June 2003. The first longer surviving (>30 days) yellow-rumped cacique were bred there since August 2007. Altogether 31 yellow-rumped caciques hatched and 18 lived from longer than one month to still living with over 16 years. However, this article aims to portray the more natural breeding and raising of yellow-rumped cacique chicks in the larger hall of the AERH.

In the AERH, while initially trying to imitate conditions known from the wild, we lacked several male birds to create a colony structure. Also, in order to spare our birds intense intraspe-

Fig. 3: Nest and its location in the hall, in a pigeon berry (*Duranta repens*) bush, next to the visitor boardwalk. Photo: T. Breuer

cific competition, we decided to initially house only one male with four females in the hall since 26.5.21. Breeding activities in 2021 were limited to short courtship rituals and the gathering of nesting material. As expected, there were no signs of serious intentions. One of the four females went missing by late November 2021, she may have escaped due to an external servicing company leaving a double door open at ground level. In early 2022 another female died by drowning in the shallow waterfall pond in the hall. The remaining two female yellow-rumped caciques showed the first signs of serious breeding activity as early as February 2022, and the nests were completed in a short time. As the vegetation had not yet grown very tall in the hall, the birds had to choose a relatively low evergreen shrub, initially 2 m and later grew to 4 m in height, a pigeon berry (*Duranta repens* syn. *D. erecta*) to build their nests (Fig. 3). This by now larger shrub/small tree with fine stems and leaves for attachment of the nests has remained the only for breeding since. The birds build their long woven nests primarily from fresh long blades of grass provided to them and fibers they pick themselves from palms (*Washingtonia robusta*) growing in the hall, which they artfully weave into a pouch-shaped nest up to 50 cm long. At the end of February 2022, we suspected that the yellow-rumped cacique had eggs, as a female was constantly disappearing into the nest. In mid-March, we heard chirping and begging noises coming from the nest. However, on March 21, 2022 we found a dead chick outside the nest, which was otherwise empty. The cause of the breeding failure could not be determined. Despite the loss of the chick, the female immediately began nest building, laying and incubating again. On April 16, 2022, the next two chicks hatched. Unfortunately, they were predated and consumed on the same day by the Guira cuckoos. Once again, the nest was rebuilt the next day and the male began to court the female. The brood that followed immediately in May 2022 ended with the death of the only young bird shortly after it fledged on June 3, 2022. It drowned on June 5, 2022 in the waterfall basin. This was despite the small branches placed in the water to help fledglings climb out again. We have learned from experience that young birds apparently find it difficult to establish themselves in such a large, richly structured hall. Potential sources of accidents (e.g. a large water basin, glass panes) seem to be difficult for them to recognize.

The nest inspection on July 1, 2022 revealed that two well-fed young birds were about to fledge. This time, we decided to remove them from the nest and raise them by hand, later placing them in a separate small cage near the nest. We hoped that the parents would continue to feed the young birds through the bars to avoid having to raise them entirely by hand. Mini-

Fig. 4: Endoscope camera used for looking into the nest without destroying it. Photo: T. Breuer

mizing interaction with the animals reduces the risk of imprinting. We only had to hand-feed the young birds for three days until we could observe that the female was taking good care of her offspring and that both parents defended them fiercely as soon as anyone approached them. The young birds were so attracted to the moving food (live insects) that they began to feed independently within a few days. The young birds remained in the small cage until they were independent, when we were able to move them to a larger aviary (enclosed enclosure) on August 8, 2022. There, the young birds had the opportunity to sit under UV light every day to prevent rickets-related changes in their bone structure. In addition, they were given mineral lime and vitamins in their food on an alternating basis. Our birds are regularly given a pinch of Opti-Breed mineral mixture® and B-Pure vitaminised brewer's yeast®, both from Versele Laga, added to their diet. In addition to stabilizing the intestinal flora, a pinch of Probac Bird from Dr. Brockamp is mixed into the feed. The young birds, identified as females, were moved to our pheasantry department on September 23, 2022 to strengthen the existing group there. While we had already considered the 2022 breeding year to be over, the adult birds still fiercely defended the area around the nest, we carried out a nest inspection in December and found two eggs. Since the nests were difficult to see into and we didn't want to destroy them during nest inspection, we used an endoscope camera (Fig. 4) for a clear look inside the nest. Unfortunately, the two eggs from December 2022 had not been incubated continuously, so we removed them. We thus concluded the 2022 breeding year with two reared offspring.

While for the first successful rearing of a clutch in July 2022 we still had two adult females in the hall, both offspring hatched previously in our pheasantry, we decided that there was too much competition for breeding space and aggression and removed the older in late November 2022. So before the start of the 2023 breeding season we only had one female (breeding female 1) and one male in the AERH hall. The first two young birds hatched in March. On April 6, 2023, a nest check revealed that both young birds were fit and healthy. On April 11, 2023, we decided to partly hand-raise the nearly fledged young birds safely and separate them for further rearing. This time, however, not in a small cage near the nest, but by placing the nest with the nestlings directly in one larger separation aviary (Fig. 5), which borders the free-flight hall with its mesh. The aim was to allow continued feeding of the young birds by the mother through the mesh. Two days later, we placed the breeding female with them for better care and control of the young birds. The male continued to have contact with the female and the young birds through the mesh.

Experience has shown us that as soon as the young birds have fledged, the male drives his female across the hall to begin a new brood, while he quickly becomes aggressive towards his own young and sees them as rivals. In the separation aviary, the female has peace and thus can care for her offspring, which are also protected from their father (Fig. 6). At the end of April 2023, we were able to let the female back into the hall after the young birds had become independent. We transferred the young birds later to another institution. On May 26, 2023 and July 1, 2023 two further broods followed with together three hatched chicks, which were not cared for by their parents, since also not taken into a separation aviary. After the two failures, two young birds hatched again on August 5, 2023. As the previously hatched young birds didn't survive, we decided to give nest predators as little time as possible to plunder the nests, while still allowing for natural rearing. On August 11, 2023, we moved the nest with the almost fully-fledged young, to the aviary and hung the nest there. The experienced female remained calm, voluntarily followed her offspring through the slide connecting to the hall, visited the nest as before and cared for her young. It was advantageous to place the female and her offspring in a smaller aviary at first, so that all the birds continued to have easy access to their food and were not prevented from foraging and feeding due to excessive stress. The visitor hall is quite large and many competitors frequent the feeding areas. We concluded the 2023 breeding year with four naturally reared birds (Fig. 7).

Fig. 5: Collected nest with cacique hatchlings being installed in the separation enclosure by C. Kiesow. Photo: T. Breuer

Fig 6: Two fledged yellow-rumped caciques in the separation enclosure. Photo: T. Breuer

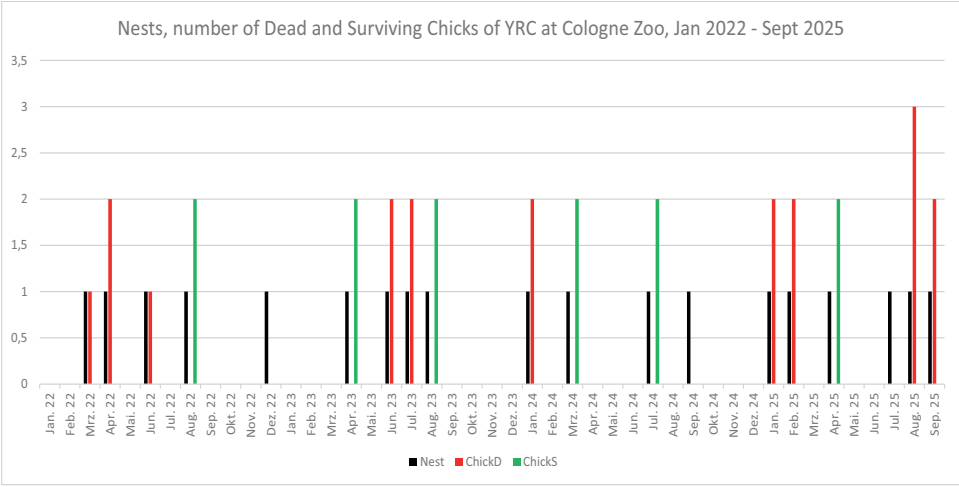

Fig 7: Time line histogram graph of nests, number of dead and surviving chicks of yellow-rumped caciques at Cologne Zoo per month between January 2022 and September 2025. Black columns= nest (Nest); red column = number of chicks seen that did not survive (ChickD); green column = number of chicks that survived (ChickS).

Breeding resumed at the beginning of 2024. Unfortunately, the first two yellow-rumped cacique chicks fell victim to the Guira cuckoos once again. However, it should be mentioned in this context that the Guira cuckoos help us to greatly reduce the unwanted house mouse (*Mus musculus*) population in the hall. The nest inspection on March 10, 2024 revealed one hatched chick and another egg in the nest. A further nest inspection on March 14, 2024 revealed that the second chick had also hatched. The birds constantly rebuild their nests to keep themselves busy and increase their breeding instinct. On March 22, 2024, we relocated the entire nest again and, as with the previous brood, placed it in one of our enclosed aviaries with the breeding female. The first chick fledged on April 4, 2024 after 26 days. The second chick followed on April 7, 2024 after 25 days. We ringed the young birds at a later date: firstly, so as not to disturb the breeding process and secondly, due to the typical nest-building behavior of the yellow-rumped cacique, as we cannot reach the newly hatched young birds without damaging the nest and finally because we have to use different sizes of rings (4.5 mm for females and 5.0 mm for males) due to the earlier described sex dimorphism. On May 24 a new nest was completed and both chicks were discovered on June 13. We took the nest with the mother on June 25 to the separation aviary were they fledged successfully (Fig. 7). In early July we discovered a Coccidia infection and had to treat the birds repeatedly for the rest of July. While we sent one of the offspring away to another institution, the other fledged chick unfortunately died in mid-July of a Coccidia infection, while the breeding female was released into the hall again in mid-August. She built a new nest and two eggs were seen on August 29, however they were found foul, being unfertilized, on September 23. This concluded the breeding season for 2024.

The breeding season 2025 started early with the female already incubating on January 5, on January 22 2 chicks were hatched, however 2 days later one chick was predated and on January 27 the nest was empty, so this brood failed. On February 12, there were two new eggs in a new nest and 12 days (24.2.25) and 16 days (28.2.25) later these hatched, however the nest was empty again on March 3. A new nesting attempt began immediately and two chicks hatched on March 29. 15 days later we moved the nest to the separation enclosure

with the female following, where the two chicks fledged 10 days later. Hereafter we decided to try breeding in this setup by alternating females in the hall with the other being busy in the separation enclosure caring for the chicks, so received a second female in mid-May from our pheasantry. This female was purchased already from a commercial bird dealer, Thomas Hoffmeister (Oelde Lette, Germany) in September 2017, which hatched in July 2016, thus already three years older than our main breeding female. She started building on the nest five weeks later and laid two eggs in early July, which disappeared before the next nest control. This female built again and on July 30 three eggs were found (Fig. 7). All three hatched on August 11, however the nest was again empty shortly later, thus predated. Only 12 days later, again three new eggs were found in a new nest built by her. Two of the chicks hatched on days 12 and 16, no information on the third egg, but then all disappeared before the next nest check. So out of her three nesting attempts in 2025, the second breeding female's eggs either disappeared shortly after laying or her chicks didn't survive long enough to be transferred with her nest and her to the separation enclosure.

After various experiments, and many failures we seem to have found a solution for breeding yellow-rumped caciques at Cologne Zoo with natural breeding and rearing of the chicks, albeit with some management intervention in our enclosures. Our experience has shown that without intervention and management of the nest and chicks there was no successful breeding possible in the larger free-flying hall.

Results of the breeding data compilation

Over 43 months of breeding activity at Cologne Zoo, with two adult females alternating towards the end, we observed that females were building nests over a period of about 12 days.

A total of 19 breeding attempts were made over a 43 months breeding activity period, thus 4 years. 17 clutches with two eggs and two clutches with three eggs were recorded, of which 16 were of one female and three of the second female. Two eggs from a single clutch in December 2025 were 29.6 mm (L) x 19.0 mm (W) with 5.51 g and 29.0 mm (L) x 19.3 mm (W) with 5.59g. We saw a total of 29 chicks initially shortly after hatching, however only 12 chicks survived. All these surviving chicks were from the first breeding female, in all four years, and always after intervention from us, by securing the chicks through moving the nest, once they were fully feathered. The second female only started to reproduce in the second third of 2025 and produced three clutches of which no chicks survived to the stage they could be moved to the security of the separation enclosure.

We could not determine the exact laying dates of eggs, due to not wanting to disturb the female on the nest with daily controls in this sensitive phase, thus no accurate data for the incubation period was determined. We estimate the incubating period as 13 days, varying between 12-16 days. However, we documented the hatching of two chicks twice, each four days apart (in March 2023 and April 2024), indicating that the eggs were also laid four days apart. Once chicks or eggs were lost due to predation of being unfertilized, a female was able to lay again within 12 days, showing a high potential for reproduction. The main nesting season was between late February to early September, with up to four nesting attempts (Fig. 7), so over the warmer half of the year, with associated greater day length, however there was also usually a nesting attempt already in December or January and February, which always failed. All nestlings that survived until they could be transferred with the nest to the separation enclosure, hatched in March or April of the years 2022-2025, or once in July 2024 in addition.

Exact fledging periods were documented five times, between 25 days (N=1) and 26 days (N=4) after hatching.

3. Discussion

The breeding records of yellow-rumped caciques in the AERH hall of Cologne Zoo illustrated a high rate of nesting and associated failed breeding attempts. This was due to manifold factors, starting from intense competition between females, disturbing each other's nest building and incubating until we reduced their numbers from four females down to one. Although yellow-rumped caciques are highly social and colonial breeders in the wild, there is also intense intrasexual competition reported (Corwin, 2020) with reports of adolescent females even abandoning nests and adolescent males harassing females and even nestlings (Robinson, 1988). This also indicates that the yellow-rumped cacique is likewise experiencing high nest failure in the wild due to manifold factors. Other factors we recorded were unfertilized eggs and clutches, but particularly egg, and nestling predation due to the high densities of predators (sloths, Guira cuckoos) but also competition. Given that one would have excluded those predators the breeding success would have been substantially higher, however few zoos could afford to have a larger free flight aviary exclusively for just a few passerine species. In addition, any naturally designed aviary will have sources of potential accidents for fledglings like bodies of water leading to their drowning with their first flight attempts or glass windowpanes leading to head strike casualties. We increased survival of nestlings by our transplantation of nest technique. We recorded mostly only two eggs per clutch, exclusively in the main breeding female and twice three eggs in the second female. Incubation lasted about 13 days, with a range of 13-16 days with some nestlings hatching up to four days apart. Fledging was 25-26 days. When looking at breeding seasonality of yellow-rumped cacique at Cologne Zoo, this was probably linked to greater day length (≥12 hours light/24 hours) and higher associated temperatures, maybe also increased access to the outside enclosure. However, there were also some earlier in the year attempts of nesting, which failed. This seasonality can be expected from a bird species from the tropics, where breeding is probably year-round but with similar day length and temperatures, however linked to slightly varying food availability. Most of the breeding biology data we collected over four years confirm what authors about yellow-rumped cacique breeding data in the wild (Jaramillo & Burke, 1999; Fraga, 2011; Corwin, 2020) have published.

4. Conclusion

A large tropical climate hall is ideal for maintaining the yellow-rumped cacique, however there must be the correct feeding regime and also nesting material (long grass and self-collected palm fibers) provided for breeding. Although a social species we have had to decrease the group size from five to only two birds, a single male and female, due to too much aggression and mutual disturbance even in a larger free-flying hall. In our experience, there are various reasons why young birds were not raised. Unfortunately, it is not possible to eliminate all risks of accidents. The best solution for us is to remove the entire nest with the almost fully-fledged young birds and their mother and house them in a separation enclosure. This simplifies daily care, as the female feeds her young, ensuring that they are raised naturally. In order to determine the right time for this move one needs to regularly check the nest with the endoscope camera. The yellow-rumped cacique is highly recommended for a planted aviary or a larger tropical hall. Their lively, sociable nature and the fact that they constantly communicate with their fellow inhabitants make these birds a great pleasure to watch. We hope to continually and successfully breed and care for this species, which has become quite rare in aviculture. Our patience and perseverance have so far been rewarded with the successful mother rearing of 12 birds, all descended from the same male with likely only one female, albeit with some management intervention

to counter nest predation and accidents of fledglings. The breeding female was bred herself in-house at Cologne Zoo in 2019 and the male came from private ownership. Even though the population of yellow-rumped caciques in Europe is still small, we hope that the species will continue to thrive in zoos and private ownership for a long time to come.

Acknowledgements

We would like to express our gratitude to our director, Prof. Theo B. Pagel, and our dedicated South America team, who constantly strive to improve our animal husbandry and thereby continuously increase our breeding success of different birds and mammals. We thank Ricarda Marr for meticulously transcribing the keepers' journal notes.

We would also like to thank Prof. Theo B. Pagel and Bernd Marcordes for proofreading and helping to improve earlier versions of the manuscript.

Zusammenfassung

Der Artikel beschreibt und analysiert die Zucht der Gelbbürzelkassike (*Cacicus cela*) im Kölner Zoo. Die Haltungsbedingungen, die Pflege, Techniken zur Steigerung des Zuchterfolgs und der Überlebensrate der Jungtiere dieser attraktiven Stärlinge (Icteridae) in einer neu erbauten Tropenhalle mit dazugehörigen Gehegen werden detailliert beschrieben. Zwischen März 2021 und September 2025 führten 19 Brutversuche zu zwölf überlebenden Nachkommen, die alle von einem einzigen Paar stammten, obwohl zunächst vier Weibchen und später ein zweites Weibchen abwechselnd eingesetzt wurden. Störungen und Nesträuber, aber auch unbefruchtete Eier und Unfälle der Jungvögel veranlassten das Team, das gesamte Nest, sobald die Jungvögel größtenteils befiedert waren, in ein separates Gehege zu verlegen, um mehr Sicherheit und Ruhe für das Weibchen und seine Nestlinge zu gewährleisten. In der Zeit zwischen Ende Februar und September wurden pro Jahr bis zu vier Nester mit Eiern oder Küken gezählt, von denen die meisten verschwanden. Die aus der Wildnis gemeldeten Brutdaten für Gelbbürzelkassiken wurden größtenteils für die Bruten im Kölner Zoo bestätigt, wobei der Nestbau zwölf Tage dauerte, die Gelegegröße zwischen zwei und drei Eiern lag, die Legezeit bis zu vier Tage auseinanderlag, die Brutzeit wahrscheinlich 13 Tage (12-16 Tage) dauerte und die Jungvögel nach 25-26 Tagen flügge wurden.

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DER ZOOLOGISCHE GARTEN
THE ZOOLOGICAL GARDEN
doi:10.53188/zg047 Zool. Garten N.F. 93 (2025) 193-196

In Memoriam

Prof. Dr. Gunther Nogge

10.01.1942 – 04.10.2025

Gunther Nogge. Foto: Christian R. Schmidt, Kronberg 2015

Pantanal (Brasilien), September 1994: «Männlicher Weißscheitel-Ameisenwürger» flüstere ich leise, damit der kleine Vogel nicht wegfliegt. Der große Professor reagiert perplex, denn meistens sage ich bei unscheinbaren Singvögeln nur lakonisch «LBJ», was so viel heißt wie Little Brown Job. Gunther Nogge, ein profunder Vogelkenner, zieht eine Braue hoch und fragt irritiert, wieso ich diesen Vogel so genau ansprechen könne? Die Antwort ist simpel: «Wir halten ein Paar der geschlechtsdimorphen Art in den Frankfurter Vogelhallen». Nach der IUDZG-(heute WAZA-)Tagung in Sao Paulo haben Gunther, seine Frau Karin und ich nicht nur den Pantanal ausgiebig erkundet, sondern auch Goldgelbe Löwenäffchen und Glockenvögel im Poco das Antas-Nationalparks aufgespürt und verschiedene Zoos sowie das Affenzentrum in

Rio de Janeiro besucht. Und Brasilien war und blieb nicht unsere einzige gemeinsame Reise. Weitere folgten, meist zusammen mit unseren Frauen. Nach einer CBSG-Tagung (Conservation Breeding Specialist Group, später CPSG) in Ocho Rios erkundeten wir gemeinsam Jamaika mit seinen zahmen Kolibris. Auch in Japan waren wir zusammen, in Singapur, Südafrika und Tansania, wo ich von Gunther sozusagen hautnah viel über Tsetsefliegen lernen durfte – seine ehemaligen Forschungsobjekte. Diese intensiven Reisen halfen uns auch ganz praxisnah, die Haltung der uns anvertrauten Tiere zu verbessern.

Gunther war es auch, der mich bei den Silverbacks (eine Gruppe pensionierter europäischer Zoodirektoren) und bei den VDZ-Silberrücken (adäquat eine Gruppe pensionierter deutschsprachiger Zoodirektoren) einführte. Unvergesslich bleibt die von ihm organisierte Exkursion nach Mecklenburg-Vorpommern, wo wir Hunderte von Kranichen auf ihrem Zug beobachten durften. Erstmals getroffen habe ich Gunther im Mai 1982 auf einer Tagung in Hannover. Fünf Jahre später, bei der 750-Jahr-Feier im Roten Rathaus in Berlin, hat er mir – der ich damals erst Kurator im Zoo Zürich (Schweiz) war – das vertraute Du angetragen. Das war damals keine Selbstverständlichkeit – im Gegensatz zu heute, wo auf EAZA-Tagungen oft junge Kuratoren wohlbestallte Zoodirektoren gleich auf Anhieb beim Vornamen nennen. Seither waren Gunther und Karin enge Freunde für meine Frau Annemarie und mich geworden. Gunther lebte mit seiner Familie mitten im Kölner Zoo in der Direktorenvilla (heute Villa Bodinus), die uns immer gastfreundlich offenstand – dies empfanden wir als Ehre. 1969 heiratete Gunther die Zoologin Karin Hempel, Sohn Oliver wurde 1973 geboren.

Den Werdegang von Gunther und seine Erfolge im Kölner Zoo habe ich schon früher ausführlich gewürdigt (Schmidt, 2002), weshalb ich dies hier nur nochmals kurz zusammenfasse. Gunther Nogge wurde am 10. Januar 1942 in Köln geboren. Diplom und Dissertation über Dasselfliegen-Larven des Rindes erfolgten 1967 beziehungsweise 1969 an der Universität Bonn. Dieses Studium brachte wenig für die erstrebte Zoolaufbahn, weshalb Gunther in den Semesterferien als Hilfstierpfleger im Kölner Zoo arbeitete. Diese praktische Erfahrung war eine wichtige Grundlage für seine spätere Arbeit im Zoo.

Von 1969 bis 1973 lehrte Gunther an der Universität Kabul (Afghanistan) im Rahmen einer Partnerschaft mit der Universität Bonn als Zoologiedozent. Zusätzlich entwickelte er den 1967 gegründeten Zoo Kabul ganz wesentlich mit (Nogge, 1973). Nach der Rückkehr von Afghanistan habilitierte er 1978 an der Universität Bonn mit einer Arbeit über Tsetsefliegen, wofür er den renommierten Insect Physiology Prize erhielt. Tsetse-Feldprojekte folgten in Tansania, Burkina Faso und Nigeria. 1983 ernannte ihn die Universität Bonn zum Professor; dort lehrte er weiterhin, bis er an die Universität zu Köln wechselte.

1981 wurde Gunther Direktor des altehrwürdigen Kölner Zoos. Obwohl Quereinsteiger in der europäischen Zooszene, führte er die traditionelle und wichtige Direktor-Morgenrunde fort. Der von ihm gegründete Förderverein «Freunde des Kölner Zoos e.V.» finanzierte schon das erste Großprojekt Urwaldhaus für Menschenaffen (1985). Weitere biologisch-tiergärtnerisch wohldurchdachte Neuanlagen entstanden für Geparden (1987), Leoparden und Irbisse (1994) und Okapis (1994). Im Jahre 2000 wurde der Regenwald für südostasiatische Tiere eröffnet; besonderes Augenmerk wurde bei dieser Anlage auf die Besucherinformation gelegt. Auch der später von der IUCN propagierte «One Plan Approach» (OPA) wurde hier bereits vorweggenommen mit direktem Bezug zu Naturschutzarbeit in Vietnam (EAZA Award for Conservation, 2006). Nicht nur für Marabus, sondern auch für Elefanten zeigte Gunther immer eine besondere Vorliebe, weshalb meine Frau und ich ihm von Reisen jeweils einen kleinen Elefanten als Freundschaftsgabe mitbrachten. Als eines seiner Meisterwerke wurde 2004 der vorbildliche Elefantenpark im Kölner Zoo eröffnet. Es war Deutschlands erste Elefantenhaltung mit «protected contact». Die Größe von zwei Hektar erlaubt die Haltung von bis zu 15 Elefanten, darunter zwei erwachsene Bullen. Zur tiergärtnerischen Qualitätsbestätigung des neuen Elefantenparks

und zur großen Freude von Gunther wurde am 30. März 2006 «Marlar» als erster Kölner Elefant geboren. Im März 2025 ist schon das 14. Jungtier zur Welt gekommen und damit die Herde der Asiatischen Elefanten im Kölner Zoo auf elf Tiere angewachsen. Im Jahre 2005 erhielt der Elefantenpark den EAZA-Award for the best exhibit. Seinem Nachfolger hinterließ Gunther einen Ganesha als Glücksbringer auf seinem Arbeitstisch (persönliche Mitteilung Theo Pagel, 16.10.2025). Die Kölner begrüßten den Umbau zum gitterlosen Zoo und pilgerten in Scharen in den Kölner Zoo, resultierend in einem Besucherrekord von über eineinhalb Millionen im Jahre 2006. Gunther wurde zur geachteten und stadtbekannten Persönlichkeit. Dank dieser Popularität stand sogar der berühmte Kölner Karneval 1985 unter dem Motto «Ene Besuch em Zoo, met jrosse und met kleine Diere».

Mit dem Ziel einer noch intensiveren Wissensvermittlung an die Besucher organisierte Gunther immer wieder Spezialausstellungen: Dinosaurier (1993 und 2003), Insekten (1995), 4 Millionen Jahre Mensch (1996), Planet Erde (1997), Wale (1999), Am Anfang war das Bild (2000), Fledermäuse (2001), Parasiten (2002), Papierwende (2004), Runter vom Holzweg (2005) und Waldmenschen (2006). Forschung war ihm immer sehr wichtig, was sich unter anderem darin zeigte, dass er den Vorsitz der EAZA-Forschungskommission übernahm (1994-2002). Neben seinen Vorlesungen an der Universität zu Köln entstanden nicht weniger als 28 Diplom- und Doktorarbeiten. Einer von seinen Doktoranden, Christoph Schwitzer, ist inzwischen Direktor im Zoo Dublin (Irland) und Chairman der European Association of Zoos and Aquariums (EAZA). Gunthers Vorträge auf Tagungen faszinierten nicht nur inhaltlich, sondern wurden als rhetorische Miniaturen geschätzt und waren geprägt von seinem trockenen Humor, der ihn ein Leben lang begleitete.

Gunther war einer der progressivsten deutschen Zoodirektoren, nicht nur wegen seiner naturnahen Neuanlagen, sondern auch in Bezug auf Bildung, Forschung und Naturschutz. Deshalb war er auch weit über Deutschland hinaus hoch angesehen. Dies zeigte sich in vielen nationalen und internationalen Ehrenämtern wie Mitglied im Beirat des WWF Deutschland, im wissenschaftlichen Beirat der Stiftung Artenschutz, im wissenschaftlichen Beirat des Instituts für Zoo- und Wildtierforschung (IZW) Berlin, im Board of Trustees des ISIS (heute Species360), im Steering Committee der Conservation Breeding Specialist Group (CBSG, heute CPSG) und als Gründungsmitglied und Vorsitzender des deutschen Komitees der Foundation King Mahendra für Naturschutz in Nepal. Eine besondere Ehrung war 2005 die Benennung des Nogge-Wasserskinks, *Tropidophorus noggei*, nach Gunther (Ziegler et al., 2005).

Besonders freut es mich, dass ich Gunther überzeugen konnte, im Juni 1985 als einziger Deutscher an einer Tagung in Antwerpen (Belgien) teilzunehmen, die zur Gründung der Europäischen Erhaltungszucht-Programme (EEP) im November des gleichen Jahres in Köln führte. Gunther lag zwar «nach einer Auseinandersetzung mit einem Schimpansen» (Nogge, 2025) zu dieser Zeit noch im Spital, eröffnete aber die Tagung im Kölner Zoo trotzdem pflichtbewusst persönlich. Was für eine unglaubliche Entwicklung von den acht EEP-Gründern zu den über tausend Teilnehmern aus 54 Ländern an der diesjährigen EAZA-Tagung in Lodz (Polen)! Gunther präsidierte die EEP-Kommission von 1987 bis 1994, und von 1998 bis 2000 war er Präsident der später gegründeten EAZA. Er erhielt 2004 sehr verdient den EAZA Award for Professional Excellence. Auch als Präsident der International Union of Directors of Zoological Gardens (IUDZG, später WAZA, World Association of Zoos and Aquariums) von 1993 bis 1995 vermittelte er wichtige Impulse für Reorganisation, Zukunftssicherung und für die Publikation der wegweisenden World Zoo Conservation Strategy. Dafür erhielt er im März 2007 in Köln feierlich die höchste Auszeichnung für Tiergärtner: den Heini Hediger Award.

Gunther blieb bis zu seinem Tod am 4. Oktober 2025 aktiv. Er erlebte noch die Publikation seines wichtigen Artikels über die von ihm wesentlich geprägte Gründung von EEP und EAZA (Nogge, 2025). Noch am 22. August 2025 gab er Mark Rosenthal (Chicago/USA) ein profundes

Interview. Das 3 Stunden 26 Minuten dauernde Interview – auf Zoo & Aquarium Video Archive aufgeschaltet – ist Gunthers letztes Vermächtnis. Sein erfülltes Leben beschrieb er in bekannt flüssigem Stil unter dem Titel Meine Zoogeschichte(n) (Nogge, 2010).

Mit Gunther Nogge verlieren wir nicht nur einen großen, aktiven und progressiven Zoodirektor und einen bedeutenden, visionären Tiergartenbiologen, sondern vor allem auch einen wunderbaren, bescheidenen Menschen und engen Freund. Lieber Gunther, es macht mich unendlich traurig, dass damit neben einer vertrauensvollen tiergartenbiologischen Zusammenarbeit vor allem auch eine großartige, 43 Jahre dauernde Freundschaft endet. Leb wohl, in meinem Herzen lebst Du weiter. Meine Gedanken sind bei Karin und Oliver.

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DER ZOOLOGISCHE GARTEN
THE ZOOLOGICAL GARDEN
doi:10.53188/zg048 Zool. Garten N.F. 93 (2025) 197-201

In Memoriam

Dr. Paul Vogt

26.06.1938 – 12.02.2025

Dr. Paul Vogt. Foto: Wolfgang Dreßen, 2023

On 12 February 2025, Dr rer. nat. Paul Vogt passed away at the age of 86 after a fulfilling and busy life. The biologist worked at Krefeld Zoo for 32 years, from 1971 to 2003, and succeeded Dr Walter Encke as director from 1996 until his retirement in 2003. His tenure as director was marked in particular by the construction and opening of the Rainforest House in 1998 – a project that was particularly close to his heart as a declared lover of South America.

Paul Vogt was born on 26 June 1938 in Laufenburg, Baden, into a family of painters. He attended the local elementary school before graduating from high school in Bad Säckingen in 1957. Subsequently, he studied biology, chemistry, and geography at Freiburg University. In 1963, he passed his state examination with a study on the optical key stimuli in dragonfly

larvae (Vogt, 1964), before completing his studies in 1967 with a doctorate at the Institute of Biology – Zoology under his doctoral supervisor Professor Dr Bernhard Hassenstein on the topic of 'Training of worker bees to sinusoidally modulated flickering light' (Vogt, 1967). He published the results of his doctoral thesis in scientific journals such as 'Naturwissenschaften' (Vogt, 1966) and 'Zeitschrift für vergleichende Physiologie' (Vogt, 1969). Paul Vogt remained close to his academic teacher, the behavioural scientist Bernhard Hassenstein, both privately and professionally until the latter's death in 2016.

After completing his university studies, Paul Vogt began to establish his first contacts with the world of zoos and in 1968 volunteered at the nearby Basel Zoo, whose horticultural concept he had always admired. He then spent two years as zoological director at the French Thoiry Animal Park near Paris under Count de la Panouse, before working as a volunteer assistant at Frankfurt Zoo under director Dr Bernhard Grzimek until 1971.

On 1 June 1971, the long-standing director of Krefeld Zoo, Dr Walter Encke, initially hired him as a research assistant before Paul Vogt was appointed Encke's deputy a year later. In his early days, he worked closely with Walter Encke to plan and design the tropical ape house, which was considered one of the most modern facilities for keeping great apes in the world when it opened in 1975 (Vogt, 1977). In the following years, the two biologists worked closely together to build a large number of animal enclosures, including the lynx enclosure and the South America Pavilion (1974), the kangaroo and mazama enclosure (1976), the Large Animal House (1977), the landscape enclosures of the European otter, serval and zebra mongoose (1980), the Hulman House (1983), the Camel Barn (1984), the Pony House (1985), the penguin enclosure (1988), the Tropical Bird House (1989) and the expansion of the 'Hausenhof' as zoo's outstation (1994/1995).

His publications during this period are diverse. An early one is about his experience with keeping and first breeding in captivity the Colombian giant toad which was discovered in 1950 and kept at Krefeld Zoo for several years from 1972 onwards (Vogt, 1974). Together with Walter Encke he was particularly interested in the keeping and breeding of snow leopards. Thanks to Encke's tireless commitment, Krefeld Zoo has been keeping this species since 1962 and cooperated closely with the zoos of Arnhem, Helsinki, and Zurich in the 1960s, 70s and 80s to establish a European breeding programme. The Krefeld facility was continuously expanded in the following years, so there were four neighbouring and interconnected enclosures by the 1980s (Vogt, 1982). Together with Walter Encke and the coordinator of the breeding programme, his Finnish colleague Leif Blomquist from Korkeasaari Zoo in Helsinki, Paul Vogt organised the 4th International Snow Leopard Symposium at Krefeld Zoo in September 1984, which attracted worldwide attention. The breeding of snow leopards remains a flagship project of Krefeld Zoo to this day, with the sixth generation of snow leopards now living there in direct succession.

Due to the breeding successes with European otters at Krefeld Zoo (Vogt, 1987), Paul Vogt became the first coordinator of the newly founded European Conservation Breeding Programme (EEP) described as a "challenging task" due to the diversity of otter husbandry in Europe and the unclear subspecies classification, until his appointment as director in 1996. He was also active in other commissions for highly endangered species in the growing European zoo community, partly due to his excellent foreign language skills. He was a member of the EEP species commissions for gorillas, maned wolves, red pandas, snow leopards, and Sumatran tigers.

When Paul Vogt took over as director of Krefeld Zoo in 1996 following the retirement of Dr Walter Encke, he had already been working there for 25 years. At the time of the handover, plans were already in preparation for a new, groundbreaking animal house, which long-time zoo patron and Krefeld benefactor Walter Gehlen wanted to bequeath to the zoo in his will. The idea of building a new tropical house 'as a miniature habitat' had been presented to Walter Gehlen by Walter Encke before his death. This project was intended to be a continuation of the

experiences gained with previous tropical houses – the Ape Tropical House opened in 1975 and the Bird Tropical House completed in 1989. Both houses were also financed by patron Walter Gehlen. However, the city administration had difficulty with Walter Gehlen's bequest of DM 4.5 million and transferred it to the 'Zoofreunde Krefeld e. V.' - the Krefeld Friends of the Zoo which now acted as the builder of the new house. This major construction project of the zoo, which was still a municipal one at that time, was therefore Paul Vogt's biggest task when he took office as director in 1996.

With its long-standing keeping of anteaters, sloths, maned wolves, bush dogs, swamp deer, guanacos, tapirs and capybaras, Krefeld Zoo had a distinct South American exotic focus in addition to its African collection. Due to the two senior zoologists' great fondness for this continent, it was clear that the new tropical house should be a rainforest house with a focus on South and Central American fauna and flora. In addition to the appropriate climatic conditions, geographically appropriate landscaping and vegetation, another important goal of the new tropical house was to make ecological relationships visible to its visitors (Vogt & Kaas, 2006).

The zoo's internal planning group started in 1993 and included Dr Encke and Dr Vogt, as well as his deputy Dr Wolfgang Dreßen and biologist Cornelia Bernhardt. Over several years, Paul Vogt visited Costa Rica in Central America, established contacts, and brought his intense knowledge of climate, soil science, hydrology and, in particular, botany to the new construction project. It was important to Paul Vogt to make clear to the visitors the natural altitude zoning and adaptations of the plants in this artificial rainforest – such as epiphytes, lianas, stranglers, and pioneer species. Several hundred plant species were planted in the house coming from Arnhem Zoo, the Botanical Gardens of Stuttgart, Bonn, and Berlin as well as from large plant nurseries in Costa Rica. After seven years, around 185 plant species from 45 families were counted in the tropical house, where most of the mammals, birds and reptiles live freely (Vogt, 1998, Vogt & Kaas, 2006). In view of the large number of animal species living in the house and the visitors, chemical pest control was avoided, especially for the plants. Supported by the entomologist Jan Piet Kaas, the pests were first identified and then 'biologically regulated' through the use of their natural enemies (Vogt & Kaas, 2006). Seven years after its opening, Vogt and Kaas were able to confirm that the Krefeld Rainforest House was in a good ecological balance. During his later visits to the zoo, Vogt always visited his tropical 'eco-display' and was always enthusiastic about the house.

The second major project under Paul Vogt's leadership was a new enclosure for big cats as the existing enclosures for Sumatran tigers, jaguars and Ceylon leopards were dilapidated and no longer complied with husbandry guidelines. The 'Mice for Cats' ('Mäuse für Katzen') campaign was very successful and contributed to the financing of the new construction project alongside the municipal contribution. It was designed by the Krefeld-based graphic design agency Finzenhagen & Partner and run by the Krefeld Friends of the Zoo. Together with Wolfgang Dreßen, Vogt designed a new stable building and outdoor enclosures for Sumatran tigers and jaguars, the latter enclosure with a steel mesh design that was used for big cats for the first time in Germany. The 'Big Cats Facility' was opened in two stages in 2002 and 2003.

The zoo's master plan, 'Entwicklungsplan 2003+' was an important document for the future of Krefeld Zoo. It was published shortly before the end of Vogt's term of office. He wrote it in close cooperation with his deputy and later successor, Wolfgang Dreßen who presented the plan to the Krefeld administration, municipal committees, and political parties in numerous meetings after its publication. It became clear that the previous legal form of Krefeld Zoo was not fit for the future requirements of a modern zoo and that it was necessary to move away from the outdated model of a municipal company.

However, Paul Vogt left the project of changing the legal form of the zoo to his successor and, when he retired in 2003, moved with his partner Walter Andreae to his hometown of Laufen-

burg in Baden. Paul Vogt remained particularly fascinated by the flora and fauna of South and Central America, especially Argentina, until the end of his life. Inspired by the travelogues of the German naturalist and explorer Alexander von Humboldt as well as the German zoologist Hans Krieg, he undertook several extended trips to the South American continent. His contacts with Argentine scientists, such as ethologist and entomologist Professor José Antonio Nunez from the University of Buenos Aires whom he had already met at the University of Freiburg as a visiting professor under his doctoral supervisor Professor Hassenstein, were helpful in this regard. Biologists Guillermo Pérez Jimeno and Mariella Superina – studbook keepers for the tamandua and zoological experts on xenarthrans, especially armadillos – also supported him on his travels. Vogt was particularly fascinated by the 'Esteros del Iberá', a marshland in northeastern Argentina, and the 'Puna de Atacama', a plateau in the interior of the Argentine Andes. Here, he visited the San Guillermo National Park, a mountain desert at an altitude of 3,000-4,500 metres, where stable populations of vicuñas, guanacos and pumas still exist (Vogt, 2013). This publication in particular highlights Vogt's geological knowledge which he acquired during his studies under the then Professor of Geography and Geology Wolfgang Weischet at the University of Freiburg. Through a series of lectures, Paul Vogt also raised money to support zoologist Emiliano Donadio who conducted etho-ecological research in this national park for many years.

Paul Vogt had a special friendship with Professor Klaus Eulenberger, the long-standing zoo veterinarian at Leipzig Zoo. The two met in 1972 at the 'International Symposium on Diseases of Zoo Animals' in Wroclaw. Despite the division of Germany, a kind of soulmate relationship and lifelong friendship quickly developed between the Eulenberger family in Leipzig and the Vogt family in Laufenburg and Krefeld. This long-standing bond was forged through regular professional exchanges and frequent mutual visits as well as a joint trip as backpackers through Argentina's wild hotspots. Klaus Eulenberger will never forget the phone call he received from Paul Vogt after the fall of the Berlin Wall and the end of the division of Germany in autumn 1989: "The border is open, come quickly to Krefeld".

Dr Paul Vogt was widely respected for his high level of expertise and his sincere commitment to the interests of Krefeld Zoo, to animal welfare and species conservation. Responsible planning of animal collection, the development of existing husbandry concepts and the preservation of Krefeld Zoo's park landscape were some of his most important premises. He spoke fluent English, French and Spanish and the "Upper-Rhine Alemannic" – a dialect that is now rarely spoken like the Swiss-German dialect of the Basel region. Paul Vogt was highly regarded by all his national and international colleagues. His Krefeld staff and many colleagues, with who he remained in contact even after his retirement, fondly remember his friendly, appreciative and always helpful manner. In the last year of his life, Paul Vogt moved to Schleswig-Holstein to live with his sister Brigitte Fawzy due to illness. He passed away peacefully there on 12 February 2025.

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Dr. Paul Vogt 2012. Foto: Wolfgang Dreßen

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Zeitschrift für die gesamte Tiergärtnerei (Neue Folge)
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DER ZOOLOGISCHE GARTEN

THE ZOOLOGICAL GARDEN

AG Zoologischer Garten Köln
Editorial Board:
DER ZOOLOGISCHE GARTEN/THE ZOOLOGICAL GARDEN
Riehler Str. 173
50735 Köln
Deutschland/Germany

Verband der Zoologischen Gärten (VdZ) e.V.
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Satz und Druck/Typesetting and Printing:
Verlag Natur & Wissenschaft Harro Hieronimus
Dompfaffweg 53
42659 Solingen

Umschlagseite/Cover:

Yellow-rumped Cacicque (*Cacicus cela*). Photo: Thomas Breuer
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VNW

DER ZOOLOGISCHE GARTEN

THE ZOOLOGICAL GARDEN

Volume 93
Issue 2 · 2025
ISSN 0044-5169

Contents/Inhalt

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