RESEARCH ARTICLE

Time to independence and predator–prey relationships of wild-born, captive-raised cheetahs released into private reserves in Namibia

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Abstract

1. Reintroduction programmes are an important tool for the conservation of threatened and endangered carnivores, but their effectiveness has rarely been assessed when wild-born, captive-raised orphans are released.

2. We monitored and evaluated the success of captive-raised orphaned cheetahs ($n = 25$) that were rehabilitated and released into the wild as adults across three private reserves in Namibia. We estimated time to independence, hunting success and prey composition, and for one reserve we derived prey preference and hunting habitat use.

3. Seventeen cheetahs achieved independence (68%) whereas eight were returned to captivity. With one exception, solitary or coalition cheetahs made their first kill 6 ± 2 days post-release. Hunting success was on average 56%, with solitary females having the highest success. We documented 13 species of wild prey killed by rehabilitated cheetahs, primarily ungulates ($n = 170$). Steenbok (*Raphicerus campestris*) were the preferred prey, although avoided by artificially formed female cheetah coalitions, which primarily killed juvenile eland (*Tragelaphus oryx*). Cheetahs used a wide range of vegetation for hunting, although coalition males appeared to use somewhat denser areas.

4. Rehabilitated wild-born captive-reared cheetahs can be successfully released if prey availability and human-wildlife conflict potential are considered, and food supplementation and intensive monitoring are undertaken.

KEYWORDS
Acinonyx jubatus, carnivore translocation, post-release monitoring, prey preference, trophic rewilding

1 | INTRODUCTION

The past century has seen severe reductions in mammal populations worldwide, particularly for the world's top predators (di Marco et al., 2014). While some species have expanded their range particularly in North America and Europe after having declined previously due to human persecution (Bruskotter & Shelby, 2010; Chapron et al., 2014), many other species especially in Asia and Africa are declining substantially (Brodie et al., 2021; di Marco et al., 2014). The cheetah (*Acinonyx jubatus*) is undoubtedly part of the latter category. The global cheetah population, once widespread throughout Africa and Asia, has experienced a period of heavy loss with numbers dropping from an estimated 100,000 individuals in the early 1900s (Marker, 1998) to approximately 7100 adult and juvenile individuals (Durant et al., 2017). This small population number has led to their current IUCN Red List status of 'Vulnerable' in most of Africa and 'Critically Endangered' in North-West Africa and Iran (Durant et al., 2022).

Namibia represents a stronghold for the cheetah and encompasses over a fifth of the global cheetah population and a third of the main southern African population of approximately 4000 adults and juveniles (Durant et al., 2017; Marker, Cristescu, Morrison, et al., 2018). However, 90% of this population exists outside protected areas and occupies private livestock and game farmland, placing cheetahs at high risk of mortality from human-wildlife conflict (hereafter, HWC) (Marker et al., 1996, 2007). Unlike many other predators, cheetahs often exhibit diurnal or crepuscular behaviour (Dröge et al., 2017) making them more likely to be seen by humans. Therefore, cheetahs stand an increased risk of mortality from lethal predator control activities. The capture of adult females with cubs by farmers often leads to killing the female and removal of the cubs from the wild. As dependent cubs (<18 months of age) are unlikely to survive on their own, countries such as Namibia transfer those cubs to conservation organisations that have the capacity and facilities to raise them. While these cubs are saved, they are still removed from the wild and thereby cease to contribute to the wild population in terms of genetic diversity and ecological role. Rehabilitation programmes have the potential to move these wild-born, orphaned cubs back into the wild once they have reached adulthood, but require rigorous protocols, monitoring and sometimes assistance to the animal especially in the first weeks following release (Walker et al., 2022).

The rehabilitation of large carnivores, including cheetahs, is not a new practice (Adamson, 1969) but has been controversial mainly due to unclear definition and low reported levels of success (Hayward et al., 2007; Hunter & Rabinowitz, 2009; Jule et al., 2008). However, with adequate selection of release candidates and post-release monitoring, independence can be achieved by a majority (75%–96%) of individuals (Walker et al., 2022). Critically, selection of appropriate release sites plays an important role in release success and can affect the survival of released individuals as well as the ability to monitor and support the released individuals (Walker et al., 2022). Destination sites for release of rehabilitated orphan cheetahs can

be selected strategically to supplement existing populations, to re-establish lost populations or facilitate population connectivity within historic cheetah range (Mills, 1991). The ability to use rehabilitated cubs that have reached adulthood for such releases avoids the impact on wild populations potentially caused by sourcing adult individuals from the wild (Josh Donlan et al., 2006).

While survival of wild-born orphaned carnivores that were released after being captive-raised and rehabilitated has been documented (Beecham et al., 2015; Kelly et al., 2010; Walker et al., 2022), little is known on the mechanisms that may facilitate the success of the rehabilitation process. In particular, predation behaviour and the composition of prey species that released carnivores are able to hunt and subdue, are important aspects that might affect release outcomes, and are possibly influenced by variability in carnivore individuals/social groups. Eurasian lynx (*Lynx lynx*) reintroduced to Switzerland consumed ungulates to a greater extent than the smaller prey species that lynx in long-term resident populations favour (Weber & Weissbrodt, 1999). When reintroduced carnivores have access to livestock, depredation can occur and may impact human attitudes towards predators as well as the success of predator releases (Gusset et al., 2008; Kolipaka et al., 2017). Factors that influence predation success and survival are complex and vary across ecological and sociological contexts (Baggio et al., 2011; Bubac et al., 2019). A functional understanding of these factors and continual post-release monitoring of released animals provide project managers with knowledge allowing for adaptive management of released carnivores towards maximising success (Hayward et al., 2007).

We analysed the post-release prey composition and hunting success of 25 wild-born, captive-raised orphaned cheetahs. The 25 cheetahs were released in 11 release events into three private reserves in Namibia between 2004 and 2012. We present parameters that we consider to be key to the success of carnivore release programmes: (i) time to independence (which indexes self-sufficiency for feeding in the release environment); (ii) prey composition and hunting success and (iii) when possible, prey preference and habitat use.

2 | METHODS

2.1 | Study animals

Twenty-five ($n_{male} = 12$, $n_{female} = 13$) of the 36 released individuals in a broader project (Walker et al., 2022), were selected for this study as they were released into private reserves (Table 1; Table S1). These wild-born, captive-raised cheetahs had been selected for rehabilitation and released as adults according to described criteria (Walker et al., 2022). The number of cheetahs included per release event ranged from one to five, with a total of 11 release events taking place between 2004 and 2012. The 11 releases consisted of coalitions ($n_{male} = 3$, $n_{female} = 3$), solitary females ($n = 4$) and a female with cubs ($n = 1$ female with four 7-month-old cubs) (Table 1). Survival analysis of these individuals was published (Walker et al., 2022).

TABLE 1 Overview of wild-born captive-raised cheetah individuals and social groups released into private reserves in Namibia as part of rehabilitation.

Individual/ group code	Individual ID (NA-AJU#)	Age at arrival (months)	Captivity time pre-release (years)	Age at release (years)	Intensive monitoring BBNO (days)	Intensive monitoring Erindi (days)	Intensive monitoring NRNR (days)	# Relocations (visual and GPS)	Release outcome
SF1	1541	11	4.0	5.0	19	N/A	N/A	668	Achieved independence
SF2	1444	4	7.0	8.0	25	N/A	N/A	229	Achieved independence
SF3	1578	6	3.5	4.0	31	N/A	N/A	488	Captivity
SF4	1560	9	3.5	4.5	31	N/A	N/A	431	Captivity
CF1	1354[a]	12	1.5	2.5	38	N/A	N/A	250	Captivity
	1355[a]	12	1.5	2.5	38	N/A	N/A	250	Captivity
CF2	1243	12	9.0	10.0	117	5	N/A	2953	Achieved independence
	1348[a]	7	7.5	8.0	117	5	N/A	3072	Achieved independence
	1349[a]	7	7.5	8.0	117	5	N/A	3005	Achieved independence
	1351[a]	7	7.5	8.0	117	5	N/A	3191	Achieved independence
CF3	1506[a]	8	2.5	3.0	N/A	N/A	0[d]	11	Achieved independence
	1507[a]	8	2.5	3.0	N/A	N/A	0[d]	360	Achieved independence
FC1[b]	1268	16	4.5	6.0	116	7	N/A	249	Achieved independence
CM1	1513[a]	14	5.0	6.0	25	N/A	N/A	867	Captivity
	1515[a]	14	5.0	6.0	25	N/A	N/A	910	Captivity
	1516[a]	14	5.0	6.0	25	N/A	N/A	874	Captivity
	1518[a]	14	5.0	6.0	25	N/A	N/A	885	Captivity
CM2[c]	1540	11	4.0	5.5	38	16	N/A	802	Achieved independence
	1545	4	3.5	4.5	38	16	N/A	1069	Achieved independence
	1561	9	3.0	4.5	38	16	N/A	1155	Achieved independence
CM3	1326[a]	3	6.0	6.0	N/A	N/A	<24	2359	Achieved independence
	1327[a]	3	6.0	6.0	N/A	N/A	<24	2359	Achieved independence
	1347[e]	7	5.5	6.0	N/A	N/A	<24	2359	Achieved independence
	1350[e]	7	5.5	6.0	N/A	N/A	<24	2453	Achieved independence
	1353	12	5.5	6.0	N/A	N/A	<24	4219	Achieved independence

[a]Sibling individuals.

[b]Female released with her 4 captive-born cubs.

[c]Coalition included one additional cheetah (1539) which was 36 months old on arrival at CCF and thereby not captive-raised.

[d]Individuals could not be monitored visually due to averse behaviour towards the monitoring vehicle and collar failure for one cheetah (NA-AJU1506).

[e]Pertains to sibling individuals.

2.2 | Release sites

The study was conducted in three geographically distinct locations in Namibia (Figure 1), chosen as being suitable cheetah habitat within the cheetah's historical range (Table S2).

Bellebenno Game Camp (BBNO) is a 36.5 km² game reserve surrounded by a game-proof (2.3 m) fence. The site is located in north-central Namibia within the Greater Waterberg Landscape and is owned and managed by the Cheetah Conservation Fund (CCF), a non-profit conservation organisation. Primary prey species for cheetah in this reserve include common duiker (*Cephalophus grimmia*), eland (*Tragelaphus oryx*), kudu (*Tragelaphus strepsiceros*), oryx (*Oryx gazella*), plains zebra (*Hippotigris quagga*), red hartebeest (*Alcelaphus buselapus*), steenbok (*Raphicerus campestris*) and warthog (*Phacochoerus*

africanus). BBNO was used as a release training camp for nine releases, comprising 19 adult cheetahs (eight male, 11 female) and four cubs. The only competing predator present in BBNO were leopards (*Panthera pardus*) at a very low density. We were unaware of any other cheetah present in the reserve during the releases.

Erindi Private Game Reserve (Erindi) is a 790 km² private ecotourism reserve surrounded by electrified game-proof fence (2.4 m). This site is located in the west-central area of the country and has some prey species that are similar to BBNO, with the additional presence of black wildebeest (*Connochaetes gnou*), blue wildebeest (*Connochaetes taurinus*) and waterbuck (*Kobus ellipsiprymnus*). Erindi held healthy populations of leopard, lion (*Panthera leo*), and spotted hyaena (*Crocuta crocuta*) during all releases. Erindi was used for three final releases comprising nine (four male, five female) of the 19
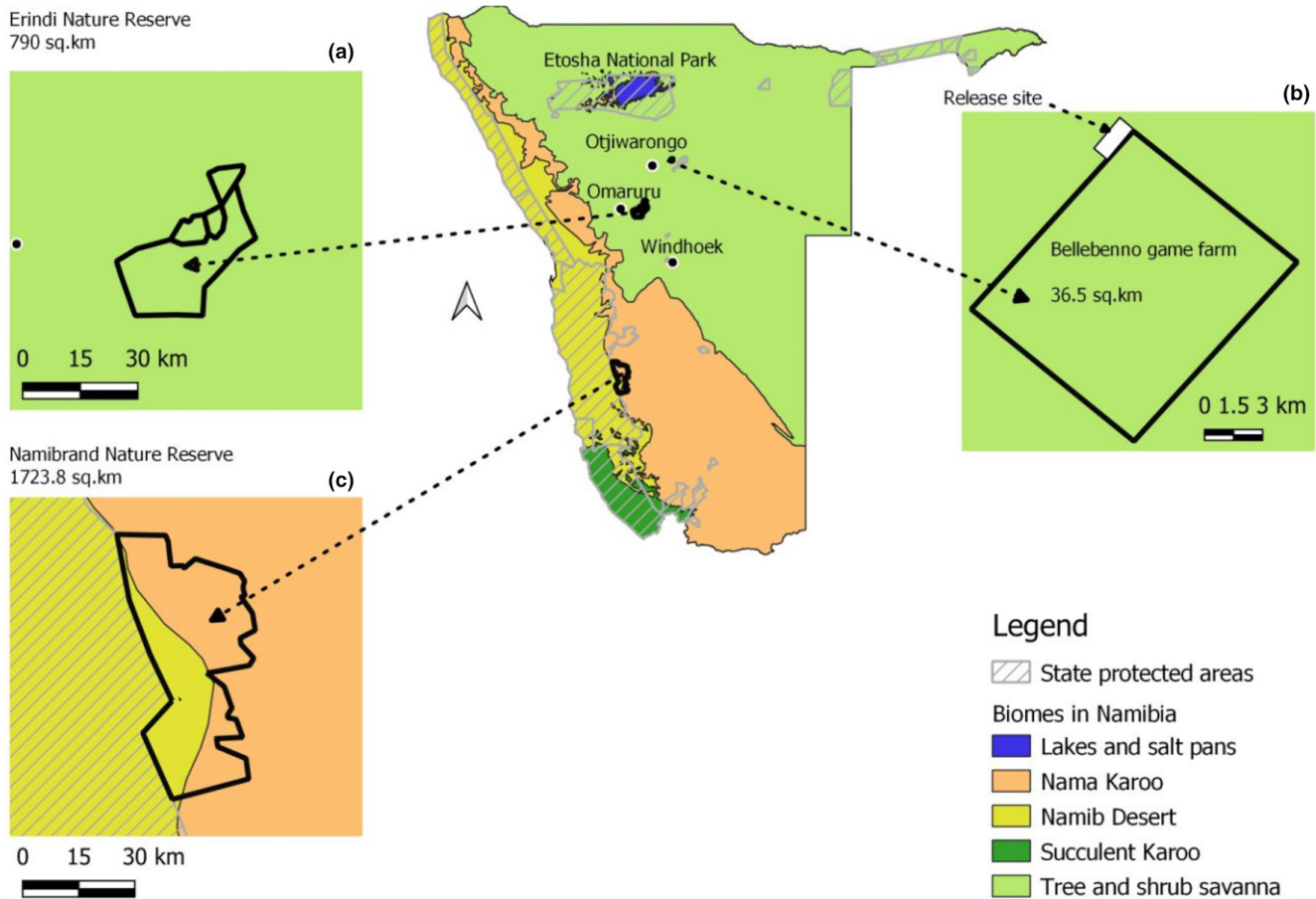
FIGURE 1 Cheetah release study areas in (a) Erindi Private Game Reserve in north-central-west Namibia, (b) Bellebenno Game Camp in north-central Namibia, and (c) NamibRand Nature Reserve in south-central Namibia. Cheetahs were rehabilitated and reintroduced between 2004 and 2012 by the Cheetah Conservation Fund.

successful adult cheetahs, and the four cubs from the BBNO training release.

NamibRand Nature Reserve (NRNR) is an un-fenced 1724 km² private reserve used for conservation and tourism. It is located in south-west Namibia adjoining the Namib Desert and is the most arid of the 3 sites. Potential prey species for cheetah include kudu, oryx, plains zebra, springbok (*Antidorcas marsupialis*), steenbok and ostrich (*Struthio camelus*). Leopard and spotted hyaena were present. NRNR was used for two releases comprising seven adult cheetahs (five male, two female).

2.3 | Pre-release management and collaring

Pre-release management (husbandry and preparation for release) are already described (Walker et al., 2022). In summary, prior to all releases, candidate cheetahs were placed in holding camps of ≥1 ha per animal that were not accessible to the public. The cheetahs were exercised daily by running after the feeding vehicle along the perimeter of the enclosure, and human contact was restricted to feeding and occasional veterinary care. Captive holding camps for all release groups were on CCF property, with the exception of CM3

which was kept in a 50 ha enclosure on a private facility in south-central Namibia. Prior to the release, diet was changed from 1 to 2 kg of meat on the bone with vitamin/mineral supplement 6 days a week, to a wild ungulate carcass every couple of days. A final health check under anaesthesia was performed prior to release to verify the health of the release candidates and place a VHF or GPS collar.

Collars were deployed on adult cheetahs using standard procedures (Marker, Schmidt-Küntzel, et al., 2018) and in accordance with relevant regulations and permits for Namibia (National Commission on Research, Science & Technology, NCRST AN202101032). Nineteen cheetahs were collared using VHF radiocollars (Advanced Telemetry Systems, Minnesota, USA) and six with Sirtrack ARGOS® GPS collars or Sirtrack Pinnacle Lite Iridium® collars (Sirtrack, Havelock North, New Zealand) (Table S1). One coalition member and the cubs released with their mother were not collared.

2.4 | Release strategy

All but two release groups were initially released into the BBNO Game Camp, where the animals could learn to become independent under

intensive supervision. Once they reached independence from supplemental feeding (i.e. no longer required supplemental feeding for survival), the successful individuals/social groups were translocated from BBNO to Erindi where they were released following a hard release strategy (without prior acclimatisation period in a holding camp). Groups CF3 and CM3 were hard released directly into NRNR.

2.5 | Post-release monitoring

All cheetahs were located from a vehicle and visually monitored after release to ensure good health, assess need for supplemental feeding, and evaluate behaviour. Visual observations were collected between 06:00 and 19:00h. We typically searched for collared cheetahs starting at dawn based on last known location (downloaded GPS coordinate, or last sighting of previous day). The GPS collars were programmed to acquire relocation fixes in a range of every 3–6h. GPS data were sent to the user via satellite connection and accessed once daily, usually between 06:00–08:00 local time to inform where to start the search. Cheetahs with VHF collars were ground-tracked using a telemetry receiver (Advanced Telemetry Systems, Minnesota, USA) and a 3-element Yaggi® antenna.

Upon locating the individual or group, we recorded time of day, GPS position for the visual observation, distance travelled since previous relocation, habitat class (open savanna ≤30%, medium/intermediate >30%–75%, or closed/dense >75% vegetation cover, Nghikembua et al., 2016), hunting attempt if observed, and whether the cheetah(s) was/were at a prey carcass. Each group was monitored with varying intensity and for different amounts of time (Table 1). Cheetahs released at BBNO were monitored intensively for the longest time as the site was located on CCF property. Animals released at Erindi and NRNR were monitored intensively by CCF staff for 1–2weeks post-release, then less frequently by Erindi and NRNR staff as part of ecotourism wildlife watching activities. Intensive monitoring involved visual relocations ≥2 times/day. Post-release monitoring was reduced once cheetahs achieved independence, defined as no longer requiring supplemental feeding for survival. After release, and until independence was reached, supplemental feeding and water were provided to all groups of cheetahs as needed (Walker et al., 2022).

2.6 | Release success

We considered releases to be successful if the cheetahs achieved independence from supplemental feeding by being able to hunt wild prey on their own and by not getting into conflict with people through killing livestock. Cheetahs that were unable to sustain their feeding requirements without repeated assistance from the post-release monitoring team and/or depredated on livestock were considered to have failed the release and were returned to captivity.

2.7 | Time to independence

Number of required supplemental feedings were recorded, and time to independence determined as the length of time between release and last supplemental feeding. One release group (CM2) and a solitary female (SF2) were released more than once, and only the data for the first release were included for calculating time to independence. Data to estimate time to independence were not available for two release groups (CF3, CM3).

2.8 | Prey composition

The diet composition of released cheetahs was estimated based on opportunistic direct observations of cheetahs making kills or cheetahs found feeding or resting at a carcass. The visual observations were made from a 4×4 vehicle and tracking on foot during post-release monitoring. The prey species and, when possible, sex, age and weight classes were assigned and recorded. Prey was divided into 3 age classes: adults (>2 years), sub-adults (1–2 years) and calves/juvenile (<1year). We categorised prey into small (<18kg), medium (18–65kg), and large (>65kg) weight classes (Mills et al., 2004) (Table S3). We considered species-specific average weights for adult and juvenile growth stages. Subadult weights were approximated using the average between adult and juvenile weights, because there was insufficient published data on subadult weights across prey species.

Although livestock (goats; $n=3$) were consumed by 2 cheetah coalitions (CF1 and CM3), we did not include domestic species in the cheetahs' prey composition because livestock were not available to consume on the reserves. Their consumption occurred when the coalitions in question escaped the protected areas, and led to the final (CF1) or temporary (CM3) return to captivity.

We used chi-square analyses to test whether there were differences in the frequencies of kills according to prey size among the three reserves. We also assessed potential differences in kill frequency by prey size among the three reproductive classes (solitary females, coalition males, coalition females). Data for FC1 were excluded due to small sample size of kills and this social group being the only female with cubs released in the study.

2.9 | Prey preference

We estimated the species-specific prey preferences of released cheetahs using Jacobs's index (Hayward et al., 2006; Hayward & Kerley, 2005; Jacobs, 1974). The index ranges from −1 to +1, with positive values indicating preference, negative values avoidance and values close to zero suggesting use proportional to availability. The Jacobs's index was estimated according to Equation (1):

$$D = \frac{r - p}{r + p - 2rp},$$

(1)

where *r* is the proportion of prey confirmed used by cheetahs and *p* the proportion of prey available to cheetahs. Calculations on prey preference were only carried out for BBNO as this was the only reserve that had data on prey availability. Prey density estimates on BBNO were available from routine annual ungulate monitoring transects performed by CCF as part of the reserve management.

We estimated prey density using distance sampling (Thomas et al., 2010), based on sighting data gathered from driving set routes (transects) within BBNO. Field crews recorded the species and group sizes of prey observed, along with perpendicular distance from the transect to the animal(s). We derived the Effective Strip Width (ESW) using package *Rdistance* in program R (R Core Team, 2023), after truncating outlier observations recorded at disproportionately large distances from the transect. We automated the run of the full suite of models available in *Rdistance* and used AICc to rank the models and to obtain the best model for deriving ESW. We then used the ESW in conjunction with prey-species specific number of observations recorded in the year when individual cheetah(s) were released, to obtain annual estimates of prey availability that were relevant for each cheetah. The number of prey individuals and percentage of each prey species killed by each cheetah group in BBNO were calculated to determine prey preference. Equivalent data were not available for the other two release sites.

2.10 | Hunting success

The hunting behaviour of all but one (CF3) cheetah groups was observed opportunistically upon visual checks on the animals. Hunting success was estimated by taking the ratio of successful hunting attempts over observed hunting attempts. We contrasted the hunting success of different cheetah reproductive classes using a chi-square test that compared observed successful versus total kill attempts. The data for the female with cubs (FC1) were excluded from statistical testing due to sample size limitations.

2.11 | Habitat use

At the BBNO site where monitoring was the most intensive, we recorded habitat use by cheetahs where the animals were observed successfully hunting prey. The habitat where the chase was initiated was visually assigned to open savanna, medium/intermediate, or closed/dense vegetation cover, as per the "Post-release monitoring" section above (Nghikembua et al., 2016). Because we did not directly quantify habitat availability in a use-available design at the scale of cheetah behavioural decisions for hunting, we could not assess hunting habitat selection as an ecological process and instead we assessed differences in patterns of hunting habitat use.

We tested for differences in habitat use by reproductive class (coalition male, coalition female, solitary female) using a Pearson's Chi-squared test of independence on the contingency table formed by the two categorical variables (reproductive class and habitat class), wherein each variable contained three levels. Due to small sample size of the cells for coalition males, we ran the test simulating *p*-values based on 2000 replicates, as not all kills had associated data on hunting habitat. Habitat use data were not recorded for social group FC1, therefore this family group was excluded from the analysis.

We performed statistical analyses in R v.4.1.0. For all chi square analyses, we first ran a regular contingency table chi square test. When sample sizes were small for some of the cells in the contingency table, we simulated *p*-values to improve the reliability of the chi-squared approximation.

3 | RESULTS

Independence was achieved by 68% (17 of 25) released wild-born captive-raised orphan cheetahs.

3.1 | Release success

3.1.1 | Unsuccessful releases

Of the nine groups released into BBNO Game Camp, four were returned to captivity as they were not deemed suitable for living in the wild (Table S1). SF3 and SF4 were returned to captivity after 1 month due to lack of interest in hunting. CF1 left the reserve after 6 weeks and were brought back into captivity as they caught a goat on a neighbouring farm and no place for release away from livestock was secured at the time. CM1 were unable to adapt to sustaining the physical strain required for hunting, due to nutritional deficiencies suffered while kept illegally as cubs by a local farmer.

3.1.2 | Successful releases

The other five groups released into BBNO Game Camp achieved independence from supplemental feeding (Table 2; Table S1). SF1 died in the wild, SF2 was returned to captivity temporarily until a suitable release site could be identified, and CF2, FC1 and CM2 were released into Erindi, where they remained until they died. CF3 and CM3 were released into NRNR, where they remained until they died.

3.2 | Time to independence

All cheetah groups, excluding FC1, made their first kill within the first 19 days of release and on average 6±2 days post-release (range=2–19) (Table 2). Required supplementary feeding events varied among individuals/social groups and ranged from 1 to 15 meals for successful releases when omitting FC1 (Table 2; Figure S1). FC1 was provided with an intensive supplemental feeding regime to

TABLE 2 Time to first kill, hunting success and prey size composition of kills made by wild-born captive-raised cheetahs released in Namibia.

Cheetah individual/ social group code[a]	Time to first kill		Hunting success			Prey size of all kills recorded (n = 183)							
	Days to first kill	# of supplemental feedings until first kill	Observed successful kills	Observed hunting attempts	Hunting success rate (%)	Large	%	Medium	%	Small	%	UNK	%
SF1	4	1	12	12	100.0	0	0.0	3	25	8	66.7	1	8.3
SF2	3	1	5	9	55.6	1	5.3	7	36.8	11	57.9	0	0.0
SF3	2	1	9	15	60.0	0	0.0	2	28.6	5	71.4	0	0.0
SF4	3	1	7	8	87.5	0	0.0	1	14.3	6	85.7	0	0.0
CF1	4	3	10	17	58.8	4	44.4	1	11.1	4	44.4	0	0.0
CF2	8	3	59	150	39.3	20	30.8	30	46.2	14	21.5	1	1.5
FC1	110	106	5	9	55.6	2	40.0	2	40.0	1	20.0	0	0.0
CM1	6	2[b]	4	50	8.0	3	50.0	2	33.3	1	16.7	0	0.0
CM2	2	1	13	28	46.4	4	21.1	5	26.3	6	31.6	4	21.1
CM3	19	15	28	57	49.1	11	32.4	8	23.5	8	23.5	7	20.6
Total			152	355	56	45	24.6	61	33.3	64	35.0	13	7.1

[a]CF3 is not included because this coalition of two females (NA-AJU1506 and NA-AJU1507) could not be monitored visually due to averse behaviour towards the monitoring vehicle and collar failure for one cheetah.

[b]CM1 was supplemental fed once, and scavenged on a carcass as a second occurrence.

support her need to raise four dependent cubs and was hence not included in the analyses.

3.3 | Hunting success

A total of 355 hunting attempts were observed of which 152 were successful. An additional 31 carcasses were found, for which hunting was not observed (and hence were not included in our analysis of hunting success), leading to a total of 183 prey animals being included in the analysis of prey composition (Figure 2). Hunting success was on average 56% but differed significantly among cheetah reproductive classes ($\chi^2 = 8.29$, df = 2, $p = 0.016$). The statistical significance was driven primarily by the high success rate of solitary females (contribution = 53%) and to a lower extent by the low success rate of coalition males (contribution = 17%). Success rate of solitary females was on average 76%, whereas coalition males achieved a mean success rate of less than half (35%).

3.4 | Prey composition

Wild prey successfully captured consisted of 13 wild species (*n* = 174), and 9 carcasses that could not be identified to species level. Most kills were ungulates (*n* = 170), whereas smaller prey including leporids (scrub hare [*Lepus saxatilis*]; *n* = 3) and carnivores (bat-eared fox [*Otocyon megalotis*]; *n* = 1) were observed to be killed infrequently. At both BBNO and Erindi reserves, the three main prey species killed were eland (calves), steenbok, and warthog (piglets), contributing 59% and 51% of kills respectively (Figure 2). In contrast, oryx, springbok and red hartebeest were the primary prey at NRNR (88%). Regardless, even though prey species composition differed at NRNR compared to the other two reserves, cheetahs killed prey of similar size classes among the three reserves ($\chi^2 = 6.43$, df = 2, $p = 0.178$).

Overall, small (35%) and medium sized prey (33%) made up most kills (Table 2). There were significant differences in kills by size class according to cheetah reproductive class ($\chi^2 = 29.40$, df = 4, $p < 0.0001$). The significance of the test was primarily driven by the disproportionately large number of small kills made by solitary females (contribution = 35%) and their low frequency of large kills (contribution = 32%). Although coalition males appeared to proportionally have the largest prey in their diet overall, the contribution of large kills by this reproductive class to the tested relationship was only 8%.

3.5 | Prey preference

Cheetahs in BBNO showed varying patterns of prey preference according to reproductive class (Figure 3). Steenbok were the preferred prey by both solitary females (*D* = 0.80) and coalition males (*D* = 0.52) but were avoided by coalition female cheetahs (D = −0.70). The latter reproductive class preferred eland (*D* = 0.39), primarily juveniles. Cheetahs generally avoided red hartebeest, plains zebra
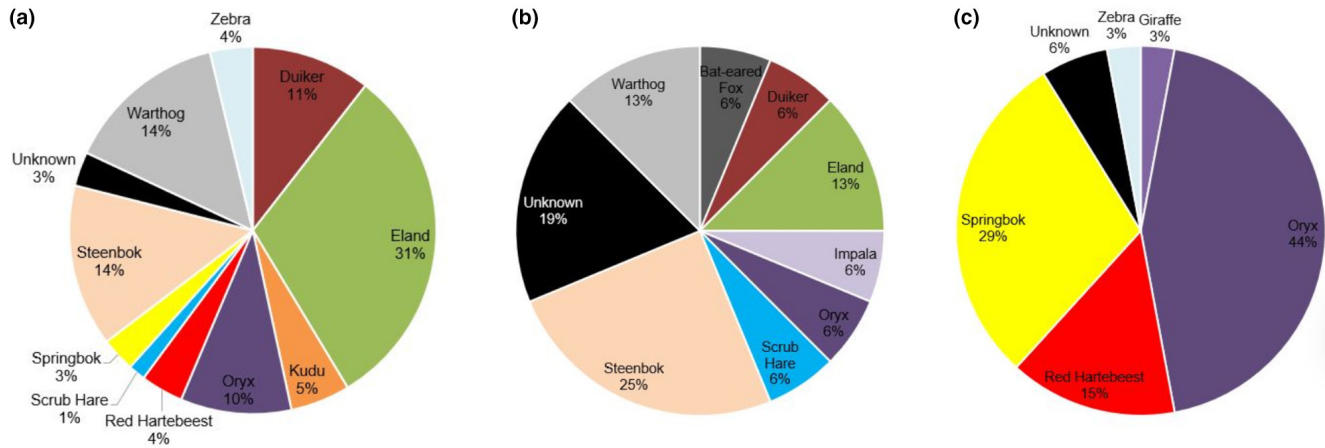
FIGURE 2 Wild prey composition of wild-born captive-raised cheetahs released into private reserves in Namibia: Bellebenno Game Camp (a; $n = 133$), Erindi Private Game Reserve (b; $n = 16$) and NamibRand Nature Reserve (c; $n = 34$).
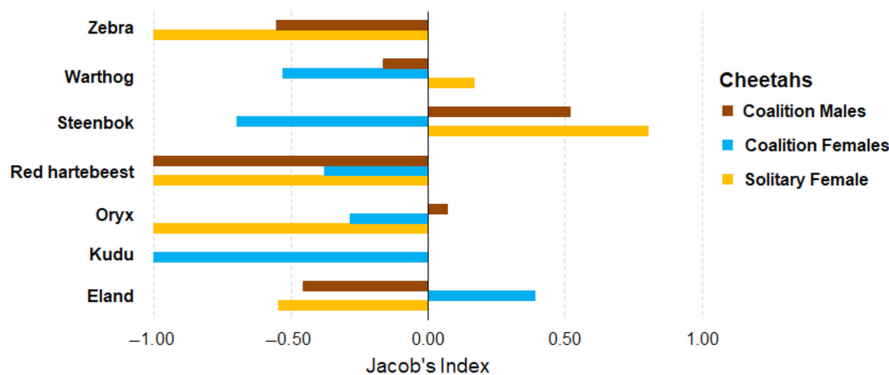

FIGURE 3 Preferred prey species of cheetah reproductive classes in Bellebenno Game Camp as revealed by Jacob's index. Positive values indicate a higher preference for the respective prey species than expected from prey availability, whereas negative values suggest avoidance. Values close to zero indicate neither preference nor avoidance.

and kudu ($D < -0.50$ with one exception), although the results for these three prey species must be interpreted with caution because these species were rarely observed, thereby affecting the reliability of density estimations. Solitary females avoided oryx ($D = -1.00$) and eland ($D = -0.54$) but somewhat preferred warthog ($D = 0.17$), primarily juveniles. In contrast, oryx were slightly preferred by coalition males ($D = 0.07$). Duiker, springbok, and scrub hare were consumed by cheetahs, but we were unable to estimate preference or avoidance for these species due to insufficient data on prey availability.

3.6 | Habitat use

Cheetahs in BBNO overall hunted in open, medium, and closed bush in relatively equal proportions based on the successful hunting events that had associated records of habitat class ($n = 109$). The chi-square test of independence trended towards significance for habitat class associated with successful hunts ($\chi^2 = 8.25$, df $= 2$, $p = 0.084$). When the data were split by reproductive class, the pattern of hunts occurring in relative equal proportions across habitats held for solitary females and coalition females. However, we did not record any kills by coalition males in open bush (Figure 4), although this finding must be treated with caution due to small sample size of kills for this reproductive class.

The data used in this paper is available at Zenodo (Marker et al., 2022).

4 | DISCUSSION

4.1 | Release success

For predators, self-sufficiency following release with regard to hunting wild prey is a critical and immediate measure of success of the release. Individuals who fail to learn associated behaviours must be returned to captivity or be provided with more training opportunities. In the cheetah releases presented here, we found that 64% of release events into reserves ($n = 7$ out of 11) were successful and that prey composition varied by cheetah socio-reproductive class. To our knowledge, this is one of the first studies to document the hunting success of rehabilitated apex predators raised in captivity from cub stage, which is important information for identifying life history adaptations of rehabilitated individuals and to assess release success. Because the distribution of large carnivores is critically dependent on the availability of prey (Winterbach et al., 2013; Wolf & Ripple, 2016), understanding predator–prey relationships in the context of predator release is important to inform the choice of release sites and to facilitate successful translocation and reintroduction programmes.
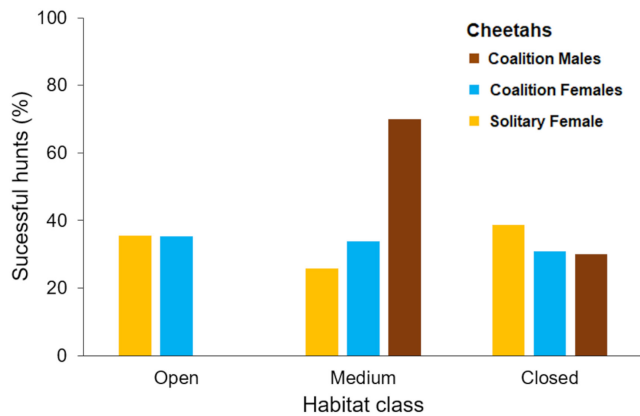
FIGURE 4 Habitat classes used by cheetahs for successful hunts in Bellebenno Game Camp ($n = 109$).

Though some cheetahs were killed by competing predators, Walker et al. (2022) found that rehabilitated cheetahs were not particularly at higher risk from competing carnivores than wild cheetahs even in areas with high competing predator density like Erindi Private Game Reserve. While release success was already high, it could have been even higher if the aim had not been to provide as many individuals as possible a chance of being released. Reasons for return to captivity for the eight cheetahs of four failed release events included lack of motivation to hunt ($n = 2$), killing livestock ($n = 2$) and insufficient fitness due to past nutritional deficiencies ($n = 4$). In light of these unfortunate events not being entirely unpredictable (in particular for the four cheetahs with insufficient fitness), we consider overall release success high, particularly given the context of using captive-raised predators for the releases.

Rehabilitation protocols that include pre-release management and post-release monitoring and feed supplementation (Walker et al., 2022) are important and we expect that they positively contributed to the release success reported here. Factors that could further improve release success include more stringent selection of release candidates, better preparation of candidates through feeding them entire carcasses in captivity earlier in the process, and longer time allowed post-release so that candidates are afforded more opportunities to become successful.

4.2 | Time to independence

Time to independence for successful cheetahs ranged from three to 17 weeks post-release and appeared to vary according to intrinsic characteristics including animal sex, social group composition, and individual behaviour. Although our sample size did not enable statistical comparison among reproductive classes, there were notable differences between male and female individuals and groups with respect to the time of first kill and total time until independence. Females appeared to require less time than males to achieve independence. A primary reason could be an inherent difference between the sexes; females in the wild are normally solitary (Caro, 1994) and

thus must be reliant on themselves for their own survival and that of their cubs, while males do not have to provide for dependents, are more social and often work in groups to hunt (Caro & Collins, 1987).

4.3 | Hunting success

Prey recognition by large carnivores is innate but learning plays a key role in successful hunting (Wang et al., 2019), which emphasises the need for post-release monitoring in carnivore rehabilitation programmes (Walker et al., 2022). In this study, most cheetahs were able to make kills relatively fast post-release, an important finding underlining the ability of apex predators to acquire necessary survival skills when provided adequate opportunities. This in turn can inform future release programmes of threatened or endangered carnivores.

Although sample sizes were insufficient for statistical analyses, we noted that within coalitions, hunting effort and success appeared to be unequally distributed. For the first 20 days, only one of the females (NA-AJU1243) of CF2 was observed to be actively hunting. Subsequently the other females began making independent kills, after which the female coalition worked together during most hunts. All members of CM2 worked together on four of their 10 observed hunting attempts, and two members (NA-AJU1540 and NA-AJU1561) were both observed hunting independently. This interindividual variation may be one of the reasons for the increased success of coalitions, as coalitions allow all group members to succeed in the wild at the same rate as the fastest learner in the coalition.

4.4 | Prey composition and preference

The prey composition of wild-born captive-raised cheetahs that we monitored after release was generally consistent with the findings of studies on the diet of wild cheetahs (Hayward et al., 2006; Marker et al., 2003). Eland (calves), steenbok and oryx (calves) were each consumed the most in one of the three study systems. Medium-sized prey was overall consumed the most, but we identified differences in prey composition among reproductive classes. Solitary females primarily consumed small prey, which they actively sought out according to the Jacobs's index; coalition females as well as the female with cubs, favoured medium size prey relative to their abundance, followed by small prey; whereas coalition males avoided large prey less than the other release groups did relative to prey abundance.

Individual variability in prey choice has been documented for apex predators (Balme et al., 2020) and is recognised to occur in many species (Cristescu & Boyce, 2013; Hayes & Jenkins, 1997). In our study, prey composition of solitary female cheetahs was similar, but there were differences in prey composition among cheetah coalitions for both sexes. For example, the proportion of large prey in the diet of CM1 and CF2 were double or more those of the other male and female coalitions, respectively. Hunting success also differed considerably among coalitions of the same sex.

4.5 | Habitat use

Cheetahs appeared to use habitat for hunting in relatively equal proportions across vegetation classes. Although bush encroachment affects cheetah habitats in many regions (Atkinson et al., 2022a), cheetahs have been shown to hunt successfully in areas affected by woody cover up to a certain threshold (Atkinson et al., 2022b). While prey catchability for a specialised cursorial predator such as the cheetah might be most efficient in open areas, vegetation cover can provide safe refuge from scavengers especially in systems where dominant carnivores that represent a potential threat to cheetahs, such as lion and spotted hyaena are absent (Atkinson et al., 2022a). We acknowledge that locations where we observed cheetahs on kills and recorded habitat class were not necessarily always the kill sites, as some of them could have been the site of prey consumption (Cristescu et al., 2022).

Although we intended to interpret time to independence, prey composition and hunting success, and prey preference and habitat use, by cheetah reproductive class in relation to the outcome of the release process (remain in the wild vs. return to captivity), we were unable to do so due to sample size limitations.

4.6 | Considerations for release practice

Releasing cheetahs in coalitions, whether they be naturally or artificially formed, can result in higher individual survival compared to releasing solitary individuals (Walker et al., 2022). Naturally formed coalitions are male coalitions formed through wild interactions, usually between related individuals, whereas artificial coalitions involve animals that are socialised in captivity through management decisions; artificial coalitions can be of either sex. One of the three male coalitions in the study (CM1) was naturally formed, whereas the other two male coalitions (CM2 and CM3) were artificially formed when they were young. All three coalitions remained fully intact throughout the release, which has been observed previously for cheetahs as well as lion prides (Hunter, 1998). The three female coalitions of this study involved two family groups (CF1, CF3) and one group composed of both related and unrelated individuals (CF2). The female coalition with individuals of mixed origin remained together, which was a surprising finding because wild female cheetahs are usually solitary. Reasons for CF2 being preserved could be that three members were sisters that had lived together for 7.5 years in captivity before release, and/or that they may not have attracted wild males as they had been chemically contracepted before release to increase their chances at success. This case demonstrates that females can maintain coalitions at least for a short period of time, and pre-bonding individuals of either sex in coalitions is worth integrating into pre-release management plans when possible, as it may increase the success of releases, for example allowing the hunt of larger prey items and improving the defence ability against inter-specific competitors. This applies equally to release groups mimicking natural social groupings (e.g. male cheetah coalitions) and those differing from natural social groupings (e.g. release of female coalitions while cheetah females tend to be solitary).

Given the differences in time to independence and hunting success as well as prey preference discussed in this study, release strategies should expect that for predator species some individuals/ social groups might take longer to achieve success in the wild than others. Decisions such as food supplementation need to be based on individual circumstances and will ultimately influence success versus return to captivity. In some cases, the first attempt to rehabilitate and release a cheetah or other large carnivore may not be an instant success, and an adaptive strategy may offer the animal(s) a second chance in the wild. Post-release monitoring is essential to enable detection of behavioural issues and facilitate effective intervention for feeding and medical care (Hunter, 1998; Mills, 1991; Walker et al., 2022). For example, intensive monitoring in our programme resulted in the initial release being halted for CF1 and CM3 because the members of both coalitions dispersed from their distinct release sites and entered neighbouring farmland, causing HWC, despite the release sites being thought to contain adequate prey and not to be saturated with cheetahs. No alternative release site could be identified for the female coalition and the risk of repeated departure from the initial release site could not be eliminated due to the small size of the release site and imperfect fencing, resulting in a final return to captivity. On the other hand, the release site of the male coalition was larger and their movements outside the release site were consistent with natural male exploratory behaviour (Marker, Cristescu, Dickman, et al., 2018). The males were therefore released a second time in the same location, using a captive female as an 'anchor' to keep them in the desired location, which ultimately resulted in success and allowed to keep the coalition in the wild. Using captive females as 'anchor' to minimise male dispersal until a home range could be established is a worthwhile strategy which would benefit from further exploration.

Critically, the success of release events depends to a great extent on the choice of adequate release sites. Sites must have a suitable prey base and be secure with regard to human pressure. In addition to sufficient prey densities, special considerations for choice of carnivore release sites should be given to prey catchability by the released animals, such as the sizes of available prey and presence of habitats that are suited for the predator's hunting strategy. For example, release sites for cheetahs must contain year-round (i.e. not only restricted to ungulate calving season) small-medium sized prey and open habitats to accommodate the cheetah's high-speed cursorial hunting strategy. It is also crucial that project scope and site conditions facilitate efficient monitoring, such as radiocollars on released animals and site accessibility by vehicle or foot. Such criteria are frequently met in private reserves or other managed areas. The density of dominant carnivores, such as lions, leopards, and spotted hyaenas in the case of cheetah releases, must also be considered to increase chances of success.

Even when protocols are followed and release conditions are ideal, our study showed that adaptive management might be

necessary to address challenges that can occur. Based on experience from our release efforts, HWC such as livestock depredation and lack of access to the cheetahs for monitoring while on private land (Walker et al., 2022) are some of the main challenges that can be encountered, whereas human imprinting, predation by dominant carnivores, exposure to diseases, and injuries when pursuing prey might also be experienced in release projects.

5 | CONCLUSION

Apex predator releases are an important component of ecosystem rewilding, but the feasibility of using captive-raised individuals for release has rarely been assessed systematically with intensive post-release monitoring programmes. For carnivore species that have experienced range contraction and marked declines, sourcing rehabilitated animals for releases could be a relevant and untapped reservoir. We provided herein baseline information on the feeding ecology of wild-born, captive-raised large carnivores released into reserves where they were monitored intensively. Release success was high, and cheetahs included a wide range of ungulates in their diet, with solitary females hunting smallest prey and coalitions killing the largest ungulates. Solitary females appeared to be the most successful hunters, but this finding should be interpreted with caution, recognising the smaller prey size preferentially hunted by solitary females and the likely difference in vulnerability to predation among herbivores of varying sizes. The success of reintroductions for ecosystem rewilding will be facilitated by choice of adequate sites that incorporate a suitable prey base, intensive post-release monitoring and supplementation if required in early phases, as well as considering the sociobiology of apex predators.

AUTHOR CONTRIBUTIONS

Laurie Marker, Anne Schmidt-Küntzel and Bogdan Cristescu conceived the ideas and designed methodology; Laurie Marker, Eli Walker and Matti Nghikembua collected the data; Bogdan Cristescu, Eli Walker and Matti Nghikembua analysed the data; Bogdan Cristescu and Eli Walker led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

CONFLICT OF INTEREST STATEMENT

The authors are employed by the Cheetah Conservation Fund, a non-profit organisation and declare that there are no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/2688-8319.12342.

DATA AVAILABILITY STATEMENT

The data associated with this manuscript are available at Zenodo (https://doi.org/10.5281/zenodo.7496215).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Number of supplemental feedings per week for rehabilitated cheetahs that were released into three private reserves of Namibia.

Table S1. Summary information for wild-born captive-raised cheetahs included in the release study.

Table S2. Summary information for the 3 release reserves used.

Table S3. Prey size designation for each of the 3 main developmental stages of prey species* for adults (A), subadults (S) and juveniles (J).