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Effects of helicopter net gunning on the survival and movement behaviour of nilgai antelope

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ABSTRACT

Context. Research on large, terrestrial mammals often requires physical captures to attach tags or collars, collect morphological data, and collect biological samples. Choice of capture method should minimise pain and distress to the animal, minimise risk to personnel, and consider whether the method can achieve study objectives without biasing results. **Aims.** We studied how capture via helicopter net-gunning affected survival, post-capture movement patterns, and space use of exotic nilgai (*Boselaphus tragocamelus*) in southern Texas, USA. **Methods.** We estimated daily survival rates for 101 collared nilgai over 28 days, following 125 captures. We calculated mean daily movement rates and net-squared displacement for 21 recaptured nilgai for 60 days, starting 30 days before capture. **Key results.** The survival probability of 125 nilgai individuals was 0.97 (95% CI = 0.92–0.99) over the 28 days following capture, with the lowest daily survival for the day after capture ($\bar{x}$ = 0.99; 95% CI = 0.96–1.00). We observed an increase of ~65% in the mean daily movement rate of 134 m/h on the first 2 days since capture, followed by a period of reduced movement out to the 5th day before returning to pre-capture levels. Analysis of net-squared displacement for 21 nilgai showed that 17 resumed pre-capture space-use patterns within a week, whereas four individuals did not return to the pre-capture range for ≥1 month. **Conclusions.** Capture-related mortality rates for nilgai using helicopter net-gunning in our study (3%) were similar or lower than those reported for similar species captured using the same method. While we were able to detect a period of elevated movement rates, followed by a recovery period of diminished movement as a result of capture, nilgai appeared to return to typical behaviour ~6 days post-capture. Most nilgai in our study also resumed typical space-use patterns within a week of capture; however, our results suggest high individual variability in their response. **Implications.** We recommend using net-gunning from a helicopter as a method for capturing nilgai when conditions and where vegetation and topography allow. We suggest censoring data for a minimum of 7 days following capture for analyses related to survival and movement rates. For analyses relating to space use, we suggest inspecting net-squared displacement or some similar displacement analysis for each animal separately to account for individual variation in response and exclude data accordingly.

Keywords: *Boselaphus tragocamelus*, capture myopathy, mortality, movement behaviour, net-gun, net-squared displacement, survival, ungulate.

Introduction

Research on free-ranging, terrestrial large mammals often requires physical capture to attach identification markers and tracking devices (ear-tags or radio-collars), or collect biological samples. Other reasons for capture include mitigation of animal damage or disease surveillance.

Capture methods suitable for large mammals include nets (drop-net, drive net, helicopter net-gun, and rocket net), walk-in traps (corral trap, box traps), or chemical immobilisation (Schemnitz 2005). An ideal capture method is both efficient and safe for animals and humans.

Additionally, capturing should have minimal impacts on individuals such that it does not significantly bias planned analyses. For example, specific capture techniques may cause myopathy, leading to death weeks after capture for some species (Beringer *et al.* 1996; Breed *et al.* 2019), which could bias survival estimates generated from resulting data. Similarly, chemical immobilisation has been reported to affect movement rates or space use up to 10 days post-capture (Becciolini *et al.* 2019; Jung *et al.* 2019). Use of these data for estimating spatial behaviour without proper censoring could, likewise, result in biased results (Dechen Quinn *et al.* 2012). Thus, understanding the impacts of specific capture techniques on individuals may be critical, depending on study objectives.

Nilgai antelope (*Boselaphus tragocamelus*) are native to India, Nepal, and Pakistan, and were introduced into southern Texas in 1924 (Leslie 2008). Nilgai have since expanded, occupying the southern counties of Texas (Fig. 1) and northern states of Mexico (i.e. Tamaulipas, Nuevo Leon, Coahuila, and Sonora; Webber *et al.* 2006), with population estimates ranging from 36 000 to over 70 000 individuals (Traweek and Welch 1992; Blihovde 2020).

Since their introduction, nilgai have become a popular game animal because they are challenging to hunt, desirable for consumption, and as an exotic, are not restricted to harvest-season regulations. However, nilgai cause damage to livestock fences (Zoromski 2019) and compete for forage with livestock and native deer (Sheffield 1983; Hines 2016; Fulbright *et al.* 2021). Additionally, nilgai act as a host to cattle fever ticks (*Rhipicephalus microplus* and *Rhipicephalus annulatus*), which can carry protozoan parasites that cause bovine babesiosis (Cárdenas-Canales *et al.* 2011). Bovine babesiosis presents significant threats to the cattle industry and is common worldwide (Bock *et al.* 2004). The United States Department of Agriculture successfully eradicated cattle fever ticks from the USA in the mid-20th century, except for a permanent quarantine area along the Texas–Mexico border. However, outbreaks of cattle fever ticks north of the quarantine area have become common in recent years and nilgai are thought to be primarily responsible (Osbrink *et al.* 2022).

Little is known about nilgai ecology in their native or introduced ranges compared with many other species of large ungulate (Leslie 2008). With the increasing importance of nilgai to recreational hunting, animal damage, and disease transmission, the need for information on movements and basic ecology of nilgai has increased. As a result, we expect studies of nilgai that require capturing and fitting with tracking collars to become more frequent.

To gain approval for research that involves capture and handling of wildlife, investigators must demonstrate that

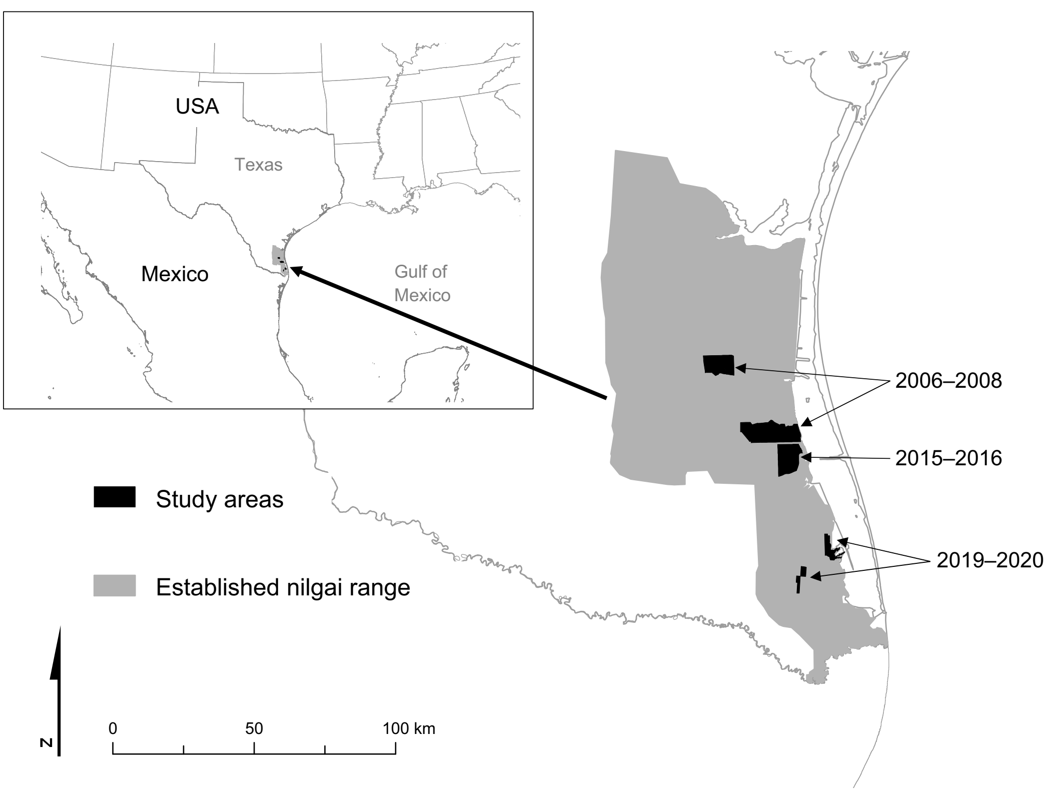

Fig. 1. Established range of nilgai (*Boselaphus tragocamelus*) in southern Texas, USA (grey), and areas where nilgai were captured for three studies (black).

the methods minimise pain and distress to the animals. In the United States, animal welfare policy for research is outlined by the Animal Welfare Act (United States Department of Agriculture (USDA) 2020), with additional guidance by the National Academy of Sciences (National Research Council 2011), and the American Veterinary Medical Association (American Veterinary Medical Association (AVMA) 2020), and recommendations from societies such as the American Society of Mammalogists (Sikes and The Animal Care and Use Committee of the American Society of Mammalogists 2016). Justification of capture techniques can be difficult for species that have received little attention. To our knowledge, there are no published guidelines for capturing and handling nilgai. Nilgai are large animals (adult males, $\bar{x}$ = 241 kg) and do not respond to feed or bait (Leslie 2008); the most common capture method on North American rangelands is the helicopter and net gun (Moczygemba *et al.* 2012; Foley *et al.* 2017). Our objective for this study was to assess the impact of capture with helicopter net-gunning on survival, movement patterns, and space use of nilgai, so as to (1) determine whether the method results in comparable mortality rates that are found to be acceptable in other ungulates, and (2) provide recommendations for censoring data for survival and movement behaviour analyses for future studies.

Materials and methods

Study area

We captured nilgai on private ranches in Kenedy, Willacy, and Cameron Counties in southern Texas (Fig. 1). The vegetation community is a mosaic of Tamaulipan thornscrub, live oak forests (*Quercus virginiana*), and open grasslands (Moczygemba *et al.* 2012; Foley *et al.* 2017). This area lies within the West Gulf Coast Plain physiographic province and contains little physical relief (Fenneman and Johnson 1946). Ranches were managed for different combinations of cattle production, wildlife, and dryland crops (sorghum and cotton). Because nilgai are exotic, there are no hunting regulations or harvest limits; they are legally considered property of the landowner, similar to cattle. Thus, nilgai were hunted year-round to varying degrees on all sites during the respective study periods.

Capture and handling

To assess impacts of capturing nilgai via net-gunning from a helicopter on survival, we combined data from three separate studies that employed the same capture methods. These included studies conducted in 2006–2008 (Moczygemba *et al.* 2012), 2015–2016 (Foley *et al.* 2017), and 2019–2020 (Sliwa 2021). Nilgai were captured using a two-seat helicopter (R22, Robinson Helicopters, Torrance, CA, USA) with a pilot and net-gunner. The pilot searched for individual nilgai and, when detected, flew at a low altitude and pushed the nilgai to an area with low vegetation, if necessary. When the nilgai was in an area of suitable terrain and vegetation, the gunner fired a net from the helicopter (Barrett *et al.* 1982).

Once netted, a ground crew using all-terrain vehicles located the animal, applied a blindfold and hobble, and removed the net. For each study, data were collected and collars were attached at the capture location; typically, nilgai were released at the capture location <15 min from the time of capture. Each captured nilgai was sexed and assigned into one of two age classes (young and adult) via tooth-wear (e.g. Severinghaus 1949). There are no formal criteria to estimate age of nilgai via tooth wear and replacement; however, sharpness of lingual crest of molars were used to distinguish between young and adult individuals (Zoromski 2019). Any nilgai that sustained an injury during capture or handling that appeared to be life-threatening (e.g. broken leg or jaw), was euthanised.

Nilgai captured during 2006 (Moczygemba *et al.* 2012) were captured in January or April and either fitted with a very high-frequency (VHF, Telemetry Solutions, Concord, California, USA) or a global positioning system (GPS; Televilt Tullus GPS, Lindesberg, Sweden) collar. Nilgai fitted with VHF collars were monitored twice a month via aircraft; GPS radio-collars recorded locations every 4 h (Moczygemba *et al.* 2012). Nilgai captured during 2015–2016 (Foley *et al.* 2017) were captured in April and fitted with GPS radio-collars (Lotek Wireless Inc., Newmarket, Ontario, Canada) that recorded locations at either 1-h or 13-h intervals. Nilgai captured in 2019–2020 were captured in March, June, or September and fitted with GPS collars programmed to record a location every hour (Vertex GPS, Vectronic Aerospace, Berlin, Germany). All capture and handling procedures were consistent with the recommendations of the American Society of Mammalogists (Sikes and The Animal Care and Use Committee of the American Society of Mammalogists 2016) and were approved by the Institutional Animal Care and Use Committee at the National Wildlife Research Center (Protocol QA-1363) or Texas A&M University–Kingsville (Protocols 2015-03-30, 2018-09-19) for Moczygemba *et al.* (2012), Foley *et al.* (2017), and Sliwa (2021) respectively.

Survival analysis

The nest-survival modelling framework in Program MARK (White and Burnham 1999) is useful for estimating survival of radio-marked animals when the exact date of mortality is unknown (Rotella *et al.* 2004). We used this framework to fit models to our data and produce daily survival estimates. The nest survival model requires the date when each individual was captured, the last date each was known to be alive, the last date each was monitored, and the fate of each individual at the end of the monitoring period. Capture-related mortality can be sudden and obvious, such as when an individual dies from trauma before it is released. Capture myopathy, caused by stress and physical exertion associated with capture, may lead to death days or weeks later (Beringer et al. 1996; Breed et al. 2019). Similarly, certain injuries sustained during capture, such as broken limb or spinal damage, are easily identified during handling, whereas injuries to internal organs or the head may go unnoticed and may eventually lead to death. We made no attempt to determine the cause of death and assumed that any non-hunting mortality within 28 days of capture was the result of capture and handling (Beringer et al. 1996; Jacques et al. 2009; Bengsen et al. 2021). We included individuals euthanised as a result of capture trauma in our capture-related survival analysis. We included covariates in our candidate models to test hypotheses that capture-related mortality rates varied between sexes, by age, linearly through time over the 28-day period, varied independent of days since capture, or were constant over the 28-day period for all animals. We used Akaike information criterion adjusted for small sample sizes (AIC_c) to identify the most parsimonious model, which we used to produce survival estimates (Burnham and Anderson 2002).

Movement analyses

Similar studies on impacts of capture on movement for red deer (*Cervus elaphus*; Becciolini et al. 2019) and roe deer (*Capreolus capreolus*; Morellet et al. 2009) have relied on location data following a single capture of individuals, requiring the authors to make assumptions regarding pre-capture behaviour (but see Neumann et al. 2011; Northrup et al. 2014; Jung et al. 2019). Foley et al. (2017), suggest that patterns of space use by nilgai are dependent on a complex social system and appear to fluctuate seasonally. Owing to our limited knowledge of nilgai ecology, we felt making assumptions of pre-capture behaviour would be imprudent. Thus, to assess the impacts of capture on the activity level and space use, we limited our analysis to the nilgai that were captured multiple times in 2019–2020, providing location data immediately before and after a capture event.

We initially captured and collared 30 individuals in March 2019; we recaptured 15 of these (four male, 11 female) in September 2019, and again recaptured six of these (two male, four female) in June 2020, for a sample size of 21 nilgai captures that we were able to record location data for immediately before and after capture. We retained only location data obtained using ≥4 satellites and excluded positions with a dilution of precision (DOP) >8 to avoid including locations with poor accuracy (D'eon and Delparte 2005). Finally, we visually inspected plots of remaining locations and removed points that appeared erroneous on the basis of extreme 1-h step lengths, coupled with large turn angles and a subsequent, similarly extreme step length back in the vicinity of the original location.

To test the hypothesis that capturing nilgai affected its movement rates, we calculated mean daily movement rates (DMR) by calculating movement rates from each hourly location (m/h) and averaging them over each 24-h period (Jung et al. 2019). We limited our analyses of movement to a 60-day period starting 30 days before capture, because we assumed that most animals would return to pre-capture behaviour and space use within 30 days following capture. This approach minimises potentially confounding impacts of seasonal changes in behaviour. We calculated the DMR from 30 days before a capture to 29 days after, averaged these calculations over all 21 nilgai, and plotted the results for visual inspection.

Net-squared displacement (NSD) is a method for describing an animal's spatio-temporal movement patterns that have been used to identify movement patterns, such as migration and dispersal (Bunnefeld et al. 2011; Singh et al. 2016). We used the NSD to further test the hypothesis that capture affected nilgai space use and movement patterns. The calculation for NSD is simply the squared straight-line distance from a specified starting point to each subsequent location. We used the centroid of all hourly locations recorded over the 30 days prior to capture for each nilgai as the starting point to which distances to each recorded location for the 60-day period straddling a capture event were calculated. We used the 30-day centroid as our starting point because we expected this to provide a suitable baseline for the range of typical movements necessary to visually detect any substantial deviation caused by a capture event. We plotted NSD against time for each nilgai individual and visually inspected them for evidence of a deviation from typical movement behaviour that correlated with the capture, as well as to determine the time to return to typical behaviour following the capture.

Results

We used data from 101 individual nilgai representing 125 captures to assess capture-related survival, including 21 individuals captured in 2006, 35 from the 2015–2016 study, and 69 captures from 45 individuals from the 2019–2020 study (29 individuals captured a single time, eight individuals captured twice, and eight individuals captured three times). The total sample included captures of 25 young and 100 adults and included 52 males and 73 females. There was a single capture-related injury in 2015 that resulted in a broken hind leg of an adult female nilgai, which was subsequently euthanised with a penetrating captive bolt gun. Three additional mortalities occurred within 28 days of a capture from the 2019–2020 study, including an adult female that died 2 days after capture, an adult female that died 3 days after capture, and a young male that died 5 days after capture. At the time the data were recorded, it was noted that the young male was bleeding from the base of its horns, suggesting the individual sustained head trauma during capture. No evidence of trauma during capture was noted, nor was the cause of death determined for the other nilgai that died in the 28 days following capture. Except for harvested animals, we did not observe any mortality that occurred between 1 and 6 months post-capture.

Survival analysis

The most parsimonious model from our daily survival analysis suggested that survival probability varied linearly over the 28-day period, receiving 0.99 of AIC_c weight among the five models we considered (Table 1). According to this model, estimated daily survival rate was lowest for the first day following capture at 0.99 (95% CI = 0.96–1.00), and increased with time (Fig. 2). The derived estimate for an individual surviving the entire 28-day period following capture from this model was 0.97 (95% CI = 0.92–0.99). Our data did not support the hypothesis that capture-related mortality varied by age or sex.

Movement analyses

The GPS location fix rates for our 21 collared nilgai over the 60-day period was >99.9% (s.e. < 0.001). We removed five points that had a reported DOP of >8 and an additional eight points that visually appeared erroneous. This resulted in 30 224 locations for the 21 nilgai. The mean DMR over the 30 days prior to capture was 134 m/h. We observed an increase of ~65% in the mean DMR to 224 m/h on the day of capture (Day 31) and 221 m/h the following day (Day 32; Fig. 3). The mean DMR appeared to return to pre-capture levels on Days 33 and 34; however, rates then dropped to 81 and 94 m/h on days 35 and 36, respectively, before returning to pre-capture levels again on day 37.

The results from our NSD analysis showed variable responses to capture by both female and male nilgai, ranging from almost no noticeable impact up to complete change in the area used that lasted weeks (Supplementary material Figs S1, S2). Although there was a noticeable increase in NSD for most nilgai associated with the time of capture, there was high variation in the magnitude of the apparent response for both males and females. Finally, even though most disruptions in NSD associated with a capture event appeared to last <1 week, there were at least two females and two males that did not return to pre-capture space-use patterns in the month following capture (Figs S1, S2).

Table 1. Model selection results for daily survival over the 28-day period following capture for nilgai (*Boselaphus tragocamelus*) captured in Texas, USA, 2006–2020.

Model[A]	ΔAIC_c	W_i[B]	k[C]	Deviance[D]
S_t	0	0.99	2	49.8
$S.$	10.1	0.01	1	62.0
S_{sex}	11.6	<0.01	2	61.4
S_{age}	12.1	<0.01	2	61.9
S_T	49.1	<0.01	28	46.5

[A]Model S_t included a covariate for a linear trend in survival through time, $S.$ assumed a constant survival rate for all individuals and across the 28-day period, S_{sex} included a covariate for sex, S_{age} included a covariate for age, and S_T allowed daily survival rates to vary for each day of the 28-day period, without assuming a relationship among days.
[B]AIC_c weights.
[C]Number of parameters.
[D]Deviance was calculated as $-2 \times \log(L)$, where L is the estimation of the likelihood for the model.

Discussion

Capturing with helicopter and net gun is the preferred method for many ungulates on rangelands (Webb *et al.* 2008; Bengsen *et al.* 2021; Beaver *et al.* 2022). However, species differ in behavioural and physiological response to capture, such that the same method may not be appropriate for all species. We observed a low mortality rate (3%) associated with capture, considering both proximate and distal causes of mortality for nilgai in our study. Mortality rates associated with net-gunning from a helicopter have been reported to be <2% for white-tailed deer (*Odocoileus virginianus*; Webb *et al.* 2008; Jacques *et al.* 2009), <4% for mule deer (*Odocoileus hemionus*; Van de Kerk *et al.* 2020), 9% for pronghorn (*Antilocarpra americana*; Jacques *et al.* 2009), and 10% for red deer in New Zealand (Latham *et al.* 2020). However, all red deer deaths associated with capture in the latter study ($n = 3$) were the result of the animals falling in steep terrain (Latham *et al.* 2020); mortality may be lower in more favourable field conditions. Our results suggested that net-gunning from a helicopter is a safe method for capturing both young and adult nilgai of both sexes. Our study has been the first evaluation of nilgai mortality associated with capture and our analysis indicated that this is an appropriate method of capture for nilgai during the conditions of our study.

Capture appeared to affect nilgai movements for several days; nilgai movement rates were elevated on the day of and the day following capture. Movement rates were within the typical range of pre-capture movement rates on 2 and 3 days following capture, then decreased to lower than typically observed on 4 and 5 days following capture. We are unaware of any other study that has identified a period of elevated movement rates, followed by a period of reduced rates. Most of the studies of impacts of capture on

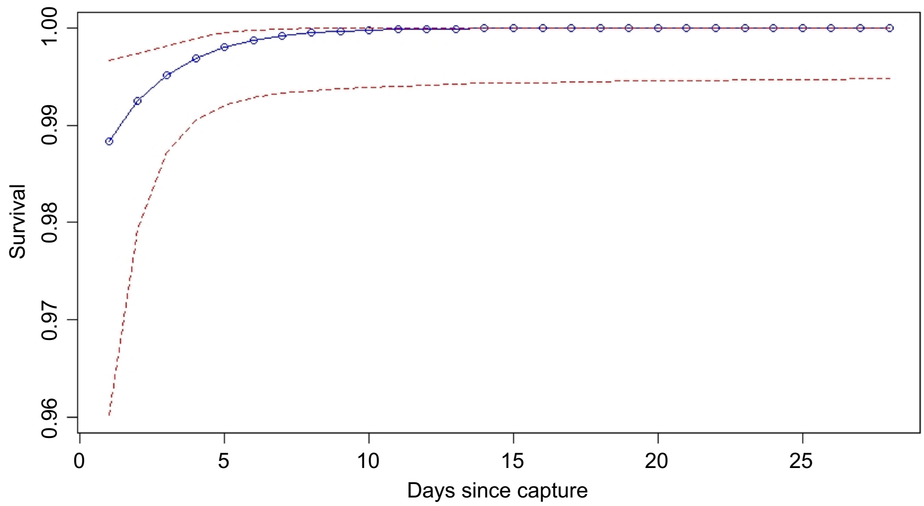

Fig. 2. Estimated daily survival rates (solid blue line) and 95% confidence interval (dashed red line) from model S_t over the 28-day period following capture for nilgai (*Boselaphus tragocamelus*) captured in Texas, USA, 2006–2020. Model S_t included a covariate that allowed survival to vary linearly over the 28-day period. Note that models were fit on the logistic scale and back-transforming estimates resulted in a slightly non-linear curve.

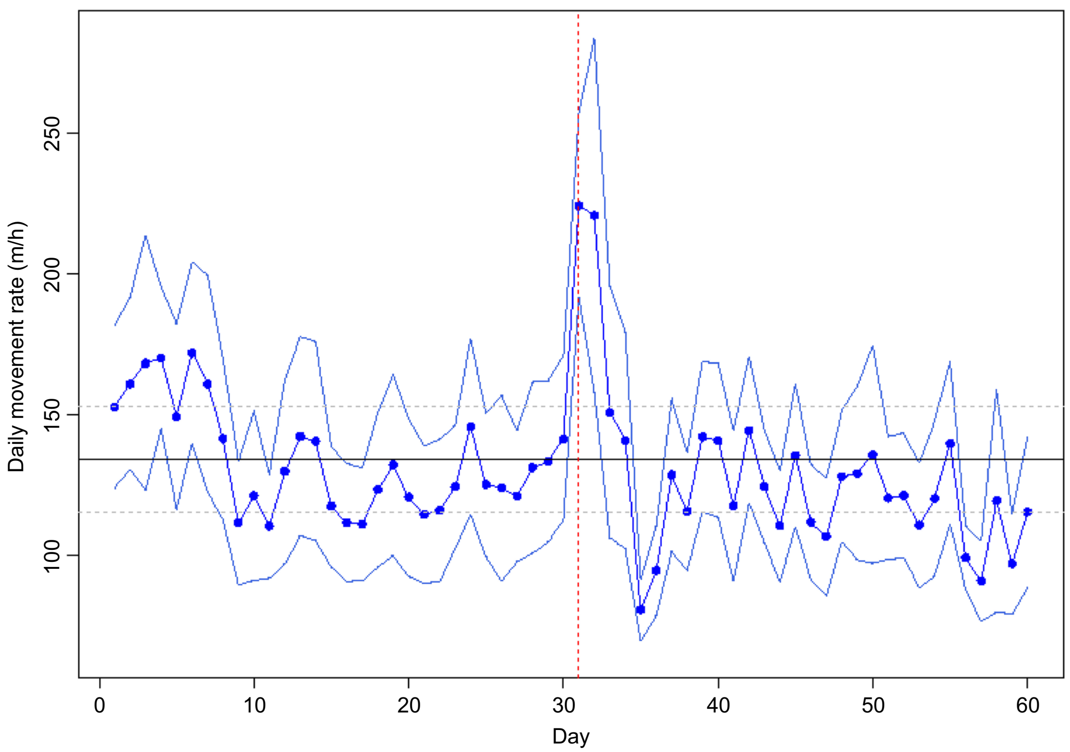

Fig. 3. Daily movement rates (DMR; blue circles) averaged over 21 nilgai (*Boselaphus tragocamelus*) captured in Texas, USA, 2019–2020. Light blue lines represent 95% confidence intervals, red dashed vertical line represents the day of capture, black horizontal solid line represents the mean DMR for all animals over the 30 days prior to capture, and grey dashed vertical lines are ±1 s.d. of mean 30-day DMR prior to capture.

large mammal movement rates that we are aware of have reported elevated movement rates lasting hours for moose (*Alces alces*; Neumann *et al.* 2011), to days for bighorn sheep (*Ovis canadensis*; Clapp *et al.* 2014), mule deer (Northrup *et al.* 2014), bison (*Bison bison*; Jung *et al.* 2019), and female red deer (Becciolini *et al.* 2019). However, reduced movement rates lasting 14 days post-capture were reported for white-tailed deer (Dechen Quinn *et al.* 2012), and Bengsen *et al.* (2021) reported fallow deer had reduced activity levels in their study lasting ~10 days after capture.

We did not chemically immobilise nilgai in our study; all animals in our movement analysis were released at the location of capture and had been collared and tagged for >6 months. Thus, we suspect the deviations we observed from pre-capture activity are directly attributable to capture and handling. Further, we suspect the elevated movement rates we observed in our released nilgai were in direct response to the capturing and handling, while the decreased rates we observed up to 5 days post-capture may represent a recovery period due to the high energy exerted over the 1–3 days post-capture.

Analysis of net-squared displacement revealed that nilgai response to capture and handling in our study ranged from undetectable to a complete shift in space used for at least a month following capture. Previous studies suggest most large mammals displaced by capture had returned to pre-capture behaviour within a week (Morellet *et al.* 2009; Neumann *et al.* 2011; Northrup *et al.* 2014; Becciolini *et al.* 2019; Jung *et al.* 2019). We are unaware of any other example from the literature of animals that were displaced from capture for more than a few weeks; however, most studies addressing this issue have lacked the pre-capture data to document such behaviour with certainty. The enduring behaviours we detected may be unique to nilgai; nilgai have relatively large home ranges (236–7069 ha) and have been documented making long-distance movements (>40 km) that were not associated with capture (Foley *et al.* 2017; Sliwa 2021).

Most studies that addressed impacts of capture and handling on movement behaviour of ungulates have involved either the use of chemical immobilisation (e.g. Neumann *et al.* 2011; Brivio *et al.* 2015; Becciolini *et al.* 2019; Jung *et al.* 2019) or releasing the study animals some distance from the location of capture (e.g. Morellet *et al.* 2009; Northrup *et al.* 2014). These additional variables make it difficult, if not impossible, to tease apart responses to capture and handling from those caused by drugs and relocating. Furthermore, studies that use single capture events and lack pre-capture data cannot separate impacts of capture from any acclimation behaviour that would have resulted from being newly fitted with GPS collars and other tags. Our study is unique in that we were able to eliminate these common variables, resulting in greater confidence that our observed impacts were solely due to capture and handling.

White and Garrott (1990) recommended excluding location data for a period of up to 1 week after capture to allow animals to acclimatise to collars and tags. Our results add to the existing body of work that has suggested that the necessary acclimation period varies by species. Furthermore, our results suggest the reported observed acclimation periods with atypical movement patterns are not entirely attributable to new collars or tags and perhaps the method of capture and handling is responsible for much of this behaviour. Indeed, Brivio *et al.* (2015) speculated that the relatively low impacts of capture on movement behaviour of ibex (*Capra ibex*) in their study were likey to be due to the low stress associated with capturing using chemical immobilisation from the ground. In a study with white-tailed deer and pronghorn captured with net-guns fired from a helicopter, Jacques *et al.* (2009) did not consider movement behaviour, but found survival improved significantly with shorter pursuit times with the helicopter and with shorter distances the animals were released from their capture locations. We recommend capturing nilgai with a net-gun fired from a helicopter based on our survival analysis. We further recommend minimising chase time and distance as much as possible because this may reduce the overall recovery behaviour and period, thus maximising location data that is not biased by atypical behaviour caused by capturing and handling. Finally, for those using data from captured and marked nilgai, we suggest censoring a minimum of 7 days following capture for analyses related to survival and movement rates. For analyses relating to space use, we agree with Neumann *et al.* (2011) and Northrup *et al.* (2014) and suggest inspecting NSD or some similar displacement analysis from each animal separately to account for individual variation in response to capture and exclude data accordingly.

Supplementary material

Supplementary material is available online.

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Data availability. The data used in this research are available at the Dryad repository under nilgai 2019 South Texas, https://doi.org/10.5061/dryad.c866t1g92.

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