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Source: Journal of Mammalogy, 100(6) : 1954-1965

Published By: American Society of Mammalogists

URL: https://doi.org/10.1093/jmammal/gyz139

*Journal of Mammalogy*, 100(6):1954–1965, 2019
DOI:10.1093/jmammal/gyz139

# Landscape-scale effects of homesteads, water, and dingoes on invading chital deer in Australia's dry tropics

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Identifying landscape features and processes that facilitate the persistence of populations is particularly important for invasive mammal species, because it can focus management interventions on relatively small areas. We used camera traps to test predictions concerning the relative abundance of invading chital deer (*Axis axis*) on seven cattle ranches in northern Australia: that abundance of chital deer would be highest near permanent water and near homesteads, and that dingoes (*Canis dingo*) reduce abundance of chital deer. Distance from the nearest homestead determined deer abundance (as indexed by images per camera-day), with negligible abundance > 4 km from homesteads. In contrast, distance from homestead did not predict abundance of feral pigs (*Sus scrofa*), macropods, or dingoes. Abundance of chital deer also declined with increasing distance from water, as did feral pig abundance. There was no relationship between either macropod or dingo abundance and distance to water. The abundance of chital deer was unaffected by dingo abundance, but 75–100% of dingo scats collected within 1 km of homesteads contained chital deer. The high abundances of chital deer near homesteads are likely due to increased food quality or quantity, or protection from dingoes, but these hypotheses require further testing. We conclude that homesteads and permanent water are important determinants of the distribution and abundance of invasive chital deer in northern Australia (i.e., they are "invasion hubs" for this species). Our results suggest that, during the dry season, managers should survey for and attempt to control chital deer within 4 km of homesteads and within 3 km of water.

Key words: artificial water points, *Axis axis*, Axis deer, biological invasions, camera trapping, diet, dingo, feral pig, invasion hubs, landscape ecology

Identifying the key landscape features and processes facilitating the persistence of populations has long been of interest to ecologists (Andrewartha and Birch 1954). This knowledge is particularly important for managing populations of invasive mammals, because it can focus management activities such as control and surveillance on relatively small areas of the landscape ("invasion hubs"—Moody and Mack 1988; With 2002; Letnic et al. 2015).

Water is likely to be particularly important for mammals invading arid and semi-arid habitats, because it enables species to persist in dry periods and subsequently expand their range during wet periods (Stafford-Smith and Morton 1990;

Choquenot and Ruscoe 2003). Predators, however, could restrict the distributions and abundances of invasive mammals, by killing them or by creating a "landscape of fear" (sensu Laundré et al. 2001) that alters their behavior, or both. Australia's top terrestrial predator, the dingo (*Canis dingo*), has a broad diet that changes with prey availability (Corbett 1995; Fleming et al. 2001; Doherty et al. 2019). Dingoes can limit the abundance of kangaroos (Caughley et al. 1980; Pople et al. 2000) and the distribution and abundance of feral goats (*Capra hircus*—Newsome 1990; Parkes et al. 1996), but their interactions with other large mammalian herbivores introduced to Australia have been little investigated (Forsyth et al. 2014, 2018, 2019).

The chital deer (*Axis axis*; males ≤ 110 kg, females ≤ 70 kg—Mattioli 2011) is native to Asia and has established non-native populations in North America, South America, Europe, Hawaii, and Australia (Long 2003). Chital deer were introduced to Australia at Maryvale, North Queensland, during the 1880s (Bentley 1998; Fig. 1). A population established and subsequently increased to an estimated 44,000 (95% confidence interval [*CI*]: 16,000–123,000) animals occupying 12,000 km$^2$ in 2014 (A. Pople and M. Brennan, aerial survey data, pers. obs.). Chital deer are grazers (Schaller 1967; Wehausen and Elliott 1982), so ranchers are concerned about potential competition for forage with beef cattle (the predominant land use in this area). High-density populations of chital deer could also transmit diseases to cattle (Davis et al. 2016; Cripps et al. 2019). Therefore, there is concern about the continued expansion of populations of chital deer in Australia (Moriarty 2004; Jesser 2005), and interest in reducing abundance within the established range (Pople et al. 2017).

The North Queensland Dry Tropics (NQDT) receives 80% of its long-term rainfall during November–March, with scarce natural water at the end of the dry season. Ranchers have therefore established artificial water points for cattle. Chital deer need to drink at least daily during hot, dry conditions (Lydekker 1907; Dunbar Brander 1923; Graf and Nichols 1966; Schaller 1967); hence, the availability of water in the late dry season could facilitate the persistence of chital deer in their invasive ranges (Ables and Fuchs 1984; Harrison 1998). Also, it has been suggested that dingoes kill chital deer (Roff 1960; Allison 1969; Bentley 1998), with the latter seldom observed "more than a few miles from the homesteads" (Roff 1960:48), possibly due to the protection homesteads provide from dingoes. Chital deer, however, have never been recorded in the diet of dingoes (Doherty et al. 2019), and Frith (1979) suggested that the aforementioned landscape features were more important determinants of chital deer distribution and abundance than dingoes.

Using camera trapping (O'Connell et al. 2011) and analyses of dingo scat contents (Doherty et al. 2019), we tested predictions about the landscape features and processes determining

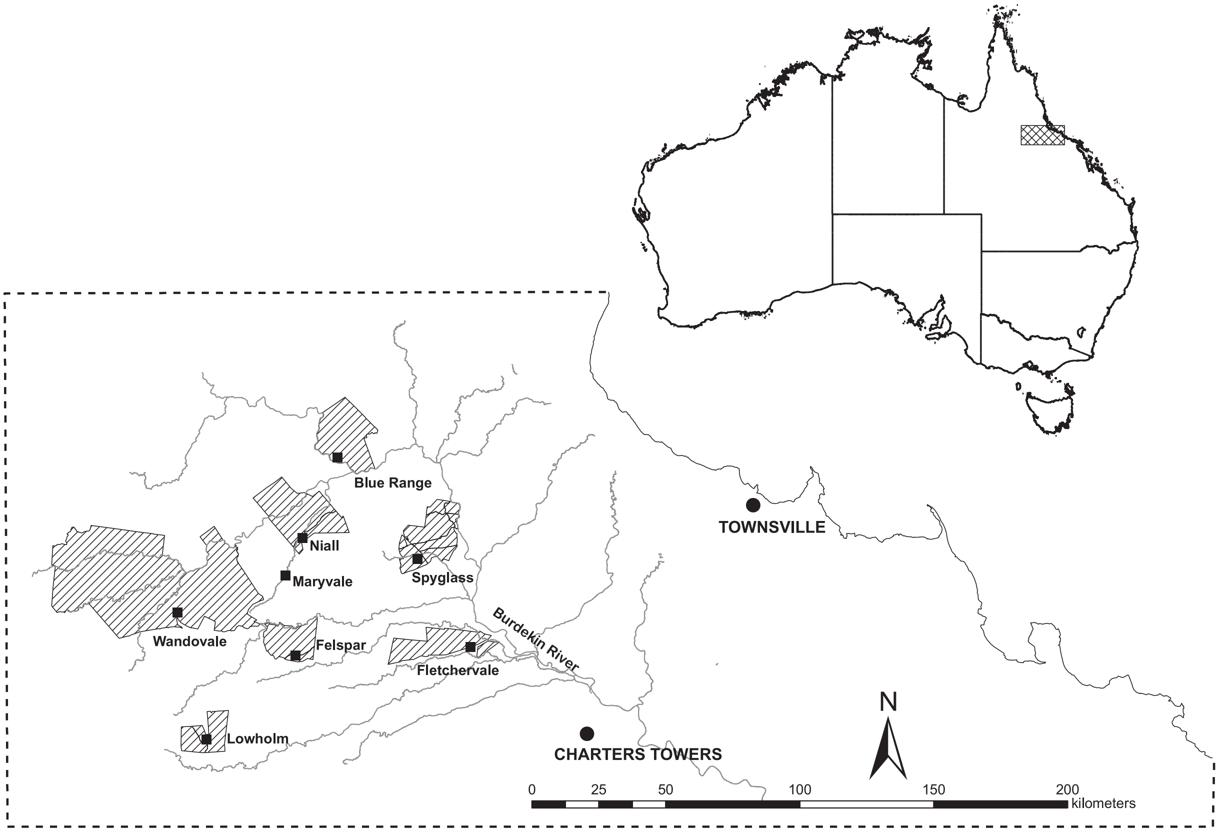

**Fig. 1.**—Locations of the seven cattle ranches (shaded) in North Queensland, Australia, where we conducted our camera and scat study in September–October 2015. Scats were also collected in November 2016. Homesteads are indicated by squares. The Maryvale homestead, where chital deer (*Axis axis*) were released in the 1880s, is also shown. Dingo (*Canis dingo*) scats were collected at the Spyglass and Niall ranches.

the relative abundance of chital deer in the NQDT during the late dry season, when water is likely to be most limiting. We first tested whether chital deer abundance declined with: 1) increasing distance from water (sensu Letnic et al. 2015), 2) increasing distance from homesteads (Roff 1960), and 3) increasing dingo abundance (Roff 1960; Allison 1969). We next quantified spatial patterns in the occurrence of chital deer remains in dingo scats. Finally, we compared the spatial patterns observed for chital deer abundance and occurrence in dingo scats with those observed for sympatric invasive feral pigs (*Sus scrofa*) and native macropods.

## MATERIALS AND METHODS

*Study area and species.*—We conducted our study on seven cattle ranches (range: 18,100–91,100 ha) in the Einasleigh Uplands bioregion of the NQDT (Fig. 1). These ranches encompass the core range of chital deer in north Queensland. The climate is semi-arid tropical with summer-dominant rainfall; however, rainfall is variable (Fig. 2) and extended dry periods are characterized by low forage availability (McIvor 2012).

Open woodlands of *Eucalyptus* spp. and *Corymbia* spp. are interspersed with patches of tussock grassland and *Acacia* and *Melaleuca* thickets. Understory species include native grasses (e.g., button grass [*Dactyloctenium radulans*], *Dichanthium* spp., and black speargrass [*Heteropogon contortus*]), introduced grasses (buffel grass [*Cenchrus ciliaris*], Sabi grass [*Urochloa mosambicensis*], and Indian bluegrass [*Bothriochloa pertusa*]), and introduced legumes (e.g., Wynn cassia [*Chamaecrista rotundifolia*] and shrubby stylo [*Stylosanthes scabra*]).

Cattle grazing (approximately one animal per 10 ha) is the primary land use in the study area (McIvor 2012). The pattern of seasonal rainfall creates an annual bottleneck in pasture and water availability for cattle during the dry season. Most ranches supplement cattle with molasses and urea during the dry season. Soil mineral deficiencies, particularly of phosphorous, force ranchers to provide dietary supplements. Earth dams and concrete troughs provide water for livestock across all ranches. Springs maintain permanent water in creeks on Fletchervale and Felspar, and there is a permanent wetland on Lowholm. The other four ranches all either adjoin or include a creek or river with permanent water.

Following their introduction at Maryvale in the 1880s (Roff 1960), chital deer colonized the seven cattle ranches as follows: Niall, early 1900s; Wandovale and Fletchervale, 1960s; Blue Range, 1970s; Felspar, 1980s; Spyglass, 1980s; and Lowholm, 1990s (M. Brennan and A. Pople, pers. obs.). There has been recreational hunting of chital deer on some of these ranches, but this is not thought to greatly affect abundance (see also Gürtler et al. 2018). Feral pigs have been present throughout the study area for many decades (Choquenot et al. 1996).

Seven species of macropods occur in the study area (Johnson 2003; A. Pople et al., pers. obs.): agile wallaby (*Notamacropus agilis*), common wallaroo (*Osphranter robustus*), eastern gray kangaroo (*Macropus giganteus*), red kangaroo (*Osphranter rufus*), allied rock-wallaby (*Petrogale assimilis*), spectacled hare-wallaby (*Lagorchestes conspicillatus*), and swamp wallaby (*Wallabia bicolor*). Macropods are considered less constrained by water availability than non-native ungulates (Lavery et al. 2018 and references therein).

Dingoes occur on all ranches, but are controlled by up to twice-yearly coordinated ground- and aerial-poison baiting (Fleming et al. 2001). Dingoes were therefore likely to have been at lower densities than they would have been in the

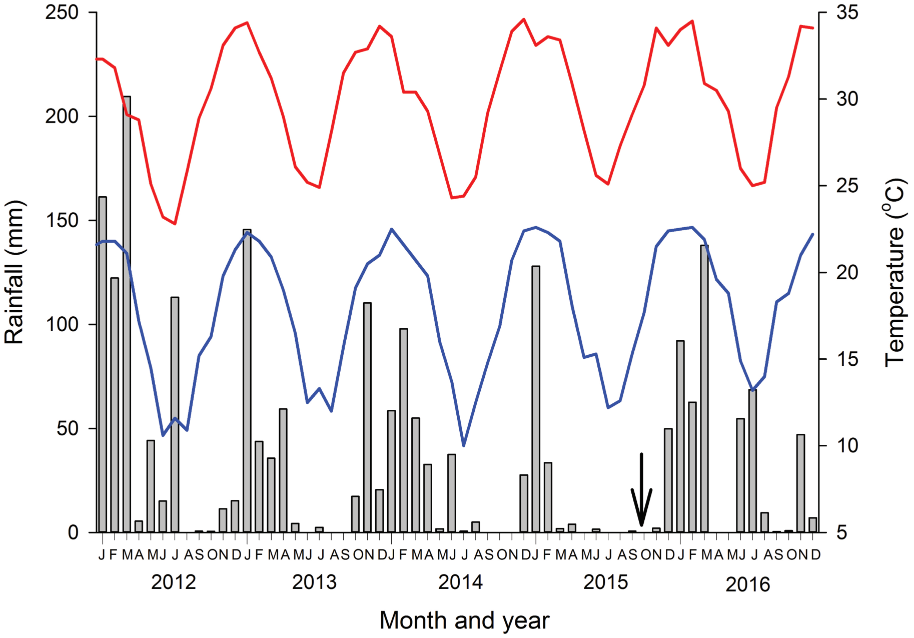

**Fig. 2.**—Monthly total rainfall (bars), and mean monthly minimum (blue line) and maximum (red line) temperatures at the Spyglass cattle ranch (see Fig. 1), North Queensland, Australia, January 2012–December 2016. Our camera study was conducted in September–October 2015 (arrowed).

absence of baiting. The frequency of baiting had varied across the seven ranches in the years leading up to this study; thus, dingo abundance was expected to vary. The diet of dingoes within the NQDT chital deer range has not been investigated; however, the diet of dingoes at Mount Stuart, ca. 200 km from our study area and outside the current range of chital deer, was dominated by agile wallaby (Allen et al. 2012).

*Camera trapping*.—We established one transect on each of the seven ranches, with the minimum distance between transects being 21 km (mean distance = 34 km). Given that the home range sizes of chital deer in our study area ranged from 8.6 to 46.5 km$^2$ (95% Minimum Convex Polygon: $n = 5$—Amos and Pople 2016), and for dingoes in the arid zone with artificial water points (i.e., similar to our study area) ranged from 37.0 to 160 km$^2$ (95% Minimum Convex Polygon) (Thomson 1992; see also Allen et al. 2017), the seven transects were considered to be independent.

We chose the origin of each camera transect in consultation with the ranch managers such that it was located as near as practical to the ranch's homestead (see Supplementary Data SD1). The direction of each transect was chosen so that cameras could be accessed by vehicle. Two remote cameras (RECONYX "Professional" or "Outdoor" models; RECONYX, Inc., Holmen, Wisconsin) were placed at the origin (0 km), and two cameras at distances of 1, 2, 4, 6, 8, and 10 km from the origin (i.e., seven pairs of cameras per transect). The two cameras within a pair were set within 100 m of each other, with each placed to view the nearest game trail. Cameras were set, unbaited, on either a tree or stake. Vegetation was pruned to provide clear detection–photographic zones for each camera. We used the "Trail" mode for both camera models (i.e., three images per detection, with 1 s between photographs and no sleep time). From previous experience, this mode was capable of photographing chital deer, feral pigs, macropods, and dingoes. The date and time were recorded on each image.

The cameras were set on 10–14 September 2015 (i.e., the late dry season; Fig. 2). Memory cards and batteries were checked and replaced after 3 weeks, with cameras removed on 27–30 October 2015. Each camera operated for 47–51 days. Our camera trapping was conducted with approval of the Department of Environment, Land, Water and Planning Animal Ethics Committee (AEC 15/08).

*Distance to nearest homestead and water.*—We determined the distances (in kilometers) from each camera pair to the nearest 1) homestead and 2) water (either a river, dam, or trough containing water), using either a hand-held GPS (GARMIN 60Csx, Garmin Ltd, Olathe, Kansas) or by analyzing spatial layers in the Queensland Spatial Catalogue (State of Queensland [Department of Natural Resources, Mines and Energy] 2018).

*Image processing.*— Data were obtained by displaying SD card images on a monitor and recording the following: camera identifier, start and end date of SD card operation, image number, date, time, and species. We calculated a daily abundance index (sensu Rovero and Marshall 2009; Parsons et al. 2017) for chital deer and each of the macropod species as the number of individuals photographed per 24 h, summed from midnight to midnight, for each camera pair. Hence, if camera A had one photo of two chital deer, and three photos of one chital deer each, and camera B had one photo with three chital deer, all within a 24-h period, then that day's chital deer abundance index would be eight. There were fewer images of feral pigs and dingoes, and a weekly abundance index was calculated for those two species.

*Dingo diet.*—While setting and retrieving the camera traps during September–October 2015, we searched for dingo scats at landscape features where this species defecates (e.g., dams, road intersections, and fences—Fleming et al. 2001) on the Spyglass and Niall ranches. To increase the scat sample size, we conducted additional searches in November 2016. Dingo scats were placed in individually labeled paper bags and sterilized at 100°C for 12 h before washing in individual nylon bags for 15 min (Johnson and Alred 1982). Scat components were identified to the lowest possible taxonomic category through comparison of remains with known reference material or the literature (Watts and Aslin 1981; Triggs and Brunner 2002), and hair identified using the technique described by Brunner and Coman (1974). Food items were recorded for each scat, and a percent volume of each prey item within the scat was visually estimated using a grid placed over the sorting tray.

*Camera abundance indices.*—The abundance index of each taxon or taxa of interest was modeled using a negative binomial general additive mixed model in a Bayesian framework. These models have been widely used to model abundance indices (Schmidt et al. 2009; Zhou et al. 2014; Russell 2015). The negative binomial model accounts for overdispersion better than equivalent Poisson models, an important consideration when the data consist of many zeros and some large values. A general additive mixed model involves a smoothed parameterization that allows for non-linear relationships between explanatory variables and the response variable, and a hierarchical structure for random effects. Let $Y_{sp,h,t,i}$ be the random variable for the number of camera observations at camera $i$ of species $sp$ at ranch $h$ on day $t$. For the taxa with daily camera abundance data (chital deer and macropods), the negative binomial modeled abundance each day at each camera pair. The mean was allowed to vary independently according to distance from the camera pair to the nearest homestead ("Homestead") and the nearest available water ("Water"), and whether the taxon or dingoes were present on the previous day. The effects of Homestead and Water were modeled using a thin-plate regression spline and linearly, respectively. The shape parameter was assumed to be consistent across cameras and ranches. The model was:

$$Y_{sp,h,t,i} \sim \text{Poisson}\left(\lambda_{sp,h,t,i} \times U\right)$$

$$U \sim \text{Gamma}\left(\nu,\ \nu\right)$$

$$\lambda_{sp,h,t,i} = e^{\eta_{sp,h,t,i}}$$

$$\begin{aligned}\eta_{sp,h,t,i} =& \beta_0 + \beta_1 \text{Water}_{h,i} + \beta_2 \text{Present}_{sp,h,t-1} \\ &+ \beta_3 \text{Present}_{\text{Dingo},h,t-1} + sm_{sp}\left(\text{Homestead}_{h,i}\right) + \varepsilon_h + \varepsilon_i \\ & sm_{sp}\left(\text{Homestead}_{h,i}\right) = \beta_4 \text{Water}_{h,i} + \omega_{sp,h,i} W_{h,i}\end{aligned}$$

$$\varepsilon_h \sim N\left(0,\, \sigma_h^2\right)$$

$$\varepsilon_i \sim N\left(0,\, \sigma_i^2\right),$$

where $Present_{sp,h,t-1}$ is an indicator function for the observed presence of species $sp$ at ranch $h$ on the previous day ($t$–1), $sm_{sp}$ is the smoother effect (Ngo and Wand 2004; Zuur et al. 2012) of the distance to homestead, and $\varepsilon_h$ and $\varepsilon_i$ are the random effects for ranch $h$ and each camera, respectively.

For feral pigs and dingoes, the negative binomial modeled the mean weekly abundance for each camera pair. Let $Y'_{sp,h,i}$ be the random variable for the total number of camera observations at camera $i$ of species $sp$ at ranch $h$. Again, the mean was allowed to vary independently according to the distance between the camera pair and the nearest homestead and water using a thin-plate regression spline and a linear model, respectively. The shape parameter was assumed to be consistent across cameras and ranches. The model was:

$$Y'_{sp,h,i} \sim \text{Poisson}\left(\lambda'_{sp,h,i} \times U'\right)$$

$$U' \sim \text{Gamma}\left(v',\, v'\right)$$

$$\lambda'_{sp,h,i} \sim e^{\eta'_{sp,h,i}}$$

$$\eta'_{sp,h,i} = \beta'_0 + \beta'_1 \text{Water}_{h,i} + sm_{sp}\left(\text{Homestead}_{h,i}\right).$$

*Predictors of chital deer, feral pig, and macropod occurrence in dingo scats.*—We tested the hypothesis that the probability of chital deer, feral pig, or macropod occurring in dingo scats varied with the same landscape-level variables that predicted the relative abundance of each of these three taxa. Due to small sample sizes for some macropod species, we pooled all macropods for this analysis. For each of chital deer, feral pig, and macropod, a binomial general additive mixed model was fitted in a Bayesian framework. The response variable was the presence of the focal taxon or taxa. As above, Water was included as a linear slope, Homestead was included as a thin-plate spline, and Ranch was included as a fixed effect.

*Model fitting, convergence, and assessment.*—All analyses were performed using JAGS (Plummer 2003) in R version 3.3.0 (R Development Core Team 2016) with the package R2jags (Su and Yajima 2015). Uninformative priors were used as the prior distribution for all parameters (see Supplementary Data SD2). Three chains were used, with a burn-in of 10,000 to ensure convergence. The convergence of the Markov chain Monte Carlo algorithm was assessed using the scale-reduction diagnostic ($\hat{R}$—Brooks and Gelman 1998), and by visual inspection of parameter trace plots. We also assessed the fit of each model using posterior predictive checks and Bayesian $P$-values (Gelman et al. 1996). All parameter estimates are shown with 95% high-density credible intervals (*HDCI*s).

## Results

*Predictors of landscape-scale chital deer, feral pig, macropod, and dingo abundance.*—The most commonly photographed species was chital deer (detected on all seven ranches), followed by eastern gray kangaroo, feral pig, common wallaroo (also all detected on all seven ranches), and agile wallaby (detected on six ranches; Table 1). Dingoes were detected on all seven ranches. For each of these species, the number of images varied greatly among ranches (Table 1).

Predictor variables that are strongly correlated (i.e., $|r| \geq 0.7$) are difficult to interpret when included in regression-type models such as we used (Dormann et al. 2013). The correlation between distance from homestead and distance from water was much less than 0.7 at five ranches ($r_{\text{sp}} \leq 0.43$), but was $\geq 0.79$ at Felspar and Spyglass (see Supplementary Data SD3). Inferences about the individual effects of distance from homestead and distance from water at those two ranches should therefore be treated cautiously.

Convergence of parameters was judged to be adequate for all models (i.e., $\hat{R} \leq 1.05$). Posterior predictive checks showed good agreement between the negative binomial model and the data for all focal taxa. The Bayesian predictive $P$-values ranged from 0.08 (chital deer) to 0.75 (feral pig). For chital deer, only three of 2,300 observations had Pearson standardized residuals > 4; for the other taxa, no Pearson residuals exceeded 4. The

**Table 1.**—Numbers of images recorded in our camera study conducted on seven cattle ranches in North Queensland, Australia, September–October 2015. There was one transect per ranch, with each transect consisting of seven pairs of cameras.

| Taxa | Total images | Number of ranches | Images per ranch |
|---|---|---|---|
| Apex mammalian predator[a] | | | |
| Dingo (*Canis dingo*) | 166 | 7 | 3–107 |
| Non-native mammalian herbivores | | | |
| Chital deer (*Axis axis*) | 2,962 | 7 | 66–754 |
| Feral pig (*Sus scrofa*) | 404 | 7 | 2–170 |
| Native macropod herbivores[b] | | | |
| Eastern gray kangaroo (*Macropus giganteus*) | 758 | 7 | 9–260 |
| Common wallaroo (*Osphranter robustus*) | 363 | 7 | 2–125 |
| Agile wallaby (*Notamacropus agilis*) | 231 | 6 | 0–197 |
| Swamp wallaby (*Wallabia bicolor*) | 14 | 2 | 0–13 |
| Spectacled hare-wallaby (*Lagorchestes conspicillatus*) | 4 | 3 | 0–2 |
| Allied rock-wallaby (*Petrogale assimilis*) | 3 | 1 | 0–3 |
| Unknown macropod | 134 | 7 | 14–61 |
| Total macropod | 1,507 | 7 | 98–364 |

[a]Red fox (*Vulpes vulpes*) and [b]red kangaroo (*Osphranter rufus*) were not detected.

random error associated with each camera location was large in comparison with the fixed parameter estimates and the random error between ranches. This large variation between cameras could be the cause of the poorer fit of the chital deer model (Table 2).

*Chital deer.*—The chital deer abundance index was explained by distance from water, distance from homestead, and whether or not they were present the previous day (Table 2; Fig. 3a–c). There was no evidence that the presence of dingoes at a camera pair one day affected deer abundance the next day (i.e., the 95% *HDCI* included zero; Table 2). Chital deer abundance declined with increasing distance from water, with lowest abundance at camera pairs furthest from water (3.0 km; Fig. 3a). There was a strong decline in chital deer abundance with increasing distance from homestead up to ~4 km; beyond this distance, chital deer abundance was extremely low (Fig. 3b). The heat map shows that the highest chital deer abundance occurred at homesteads near water (Fig. 3c). Having deer present at a camera pair the previous day increased the abundance index the next day by a factor of 3.8 (95% *HDCI*: 3.0–4.9].

*Feral pigs.*—Distance from water, but not distance from homestead, was an important predictor of feral pig abundance (Table 2; Fig. 3d–f). Feral pig abundance declined rapidly with increasing distance from water, with negligible abundance at > 1.0 km from water.

**Table 2.**—Parameter estimates (all log scale, except for variances and shape parameters) for the negative binomial models of chital deer (*Axis axis*), feral pig (*Sus scrofa*), macropod, and dingo (*Canis dingo*) abundance indices at seven cattle ranches in North Queensland, Australia, September–October 2015. Distance from homestead was included as a predictor variable using a thin-plate regression spline, but has too many parameters to include here; see the modeled relationships in Fig. 3. The medians and lower and upper bounds come from the 95% high-density credible intervals for the posterior distributions.

| Taxon | Parameter | 2.5% | Median | 97.5% |
|---|---|---|---|---|
| Chital deer (*Axis axis*) | Intercept | –3.463 | –2.779 | –2.087 |
| | Distance from water | –0.702 | –0.503 | –0.311 |
| | Dingo present previous day | –0.553 | –0.113 | 0.343 |
| | Deer present previous day | 1.085 | 1.341 | 1.596 |
| | $\sigma_{\text{Camera}}^2$ | 1.63 | 2.05 | 2.42 |
| | $\sigma_{\text{Ranch}}^2$ | 0.11 | 0.32 | 1.58 |
| | Shape | 2.54 | 17.09 | 64.91 |
| Feral pig (*Sus scrofa*) | Intercept | –4.347 | –3.153 | –1.870 |
| | Distance from water | –2.235 | –1.492 | –0.752 |
| | Shape | 0.242 | 0.451 | 0.865 |
| Macropod | Intercept | –1.839 | –1.242 | –0.717 |
| | Distance from water | –0.618 | –0.476 | –0.337 |
| | Dingo present previous day | –0.087 | 0.322 | 0.737 |
| | Macropod present previous day | 1.054 | 1.286 | 1.531 |
| | $\sigma_{\text{Camera}}^2$ | 0.33 | 0.92 | 1.95 |
| | $\sigma_{\text{Ranch}}^2$ | 0.01 | 0.06 | 0.32 |
| | Shape | 0.50 | 0.93 | 16.65 |
| Dingo (*Canis dingo*) | Intercept | –4.612 | –3.344 | –2.119 |
| | Distance from water | –1.152 | –0.526 | 0.081 |
| | Shape | 0.369 | 0.813 | 1.777 |

*Macropods.*—Distance from water and distance from homestead were important predictors of macropod abundance (Table 2; Fig. 3g–i). Similarly to chital deer and feral pigs, macropod abundance declined with increasing distance from water (Fig. 3g). In contrast to chital deer, macropod abundance increased with increasing distance from homestead, reaching a maximum at > 6 km from homesteads (Fig. 3h). The form of the relationship was weaker, however, with moderate macropod abundance occurring at 2.5 km from water. The heat map shows that the highest macropod abundance occurred closest to water furthest from homesteads (Fig. 3i).

*Dingoes.*—The data suggested that dingo abundance declined with increasing distance from water (Fig. 3j), but the 95% *HDCI* for this parameter included zero (Table 2). The smoother for distance from homestead was flat across the range of observed values (Fig. 3k). The heat map of estimated dingo abundance index in relation to the distance to homestead and distance to water showed no discernible effect for either variable (Fig. 3l).

*Predictors of chital deer, feral pig, and macropod occurrence in dingo scats.*—We collected a total of 127 dingo scats from the Spyglass ($n$ = 76) and Niall ($n$ = 51) ranches. The most commonly occurring prey items were agile wallaby (50% frequency of occurrence [FO]), chital deer (28% FO), bird (11% FO), European rabbit (*Oryctolagus cuniculus*; 10% FO), feral pig (7% FO), and cattle (7% FO; Table 3). In scats in which they were detected, the mean (± *SD*) percentage volumes of agile wallaby and chital deer (i.e., the two most frequently detected taxa) were 73 ± 34% and 60 ± 34%, respectively.

The probability of a scat containing chital deer declined with increasing distance from water, with the odds decreasing 4-fold beyond 1 km (Fig. 4a; Table 4). The probability of a scat containing chital deer, however, declined more strongly with increasing distance from homestead (Fig. 4b). Nearly all scats within 1 km of a homestead contained chital deer, but this declined to < 25% at distances > 5 km from a homestead. The effect of distance from homestead on the probability of a dingo scat containing chital deer was therefore much stronger than that of distance from water.

Feral pigs were detected in few dingo scats, but all detections were within 200 m of water, and the probability of occurrence declined significantly with increasing distance from water (Fig. 4c; Table 4). There was no effect of distance from homestead on the probability of a dingo scat containing feral pig (Fig. 4d; Table 4).

There was no effect of distance from water or distance from homestead on the probability of detecting macropod in a dingo scat (Fig. 4e and f; Table 4).

## DISCUSSION

Chital deer have established non-native populations on several continents. We evaluated factors hypothesized to predict their landscape-scale abundance, and our analyses supported the predictions that the abundance of chital deer declined with increasing distance from homesteads and permanent water,

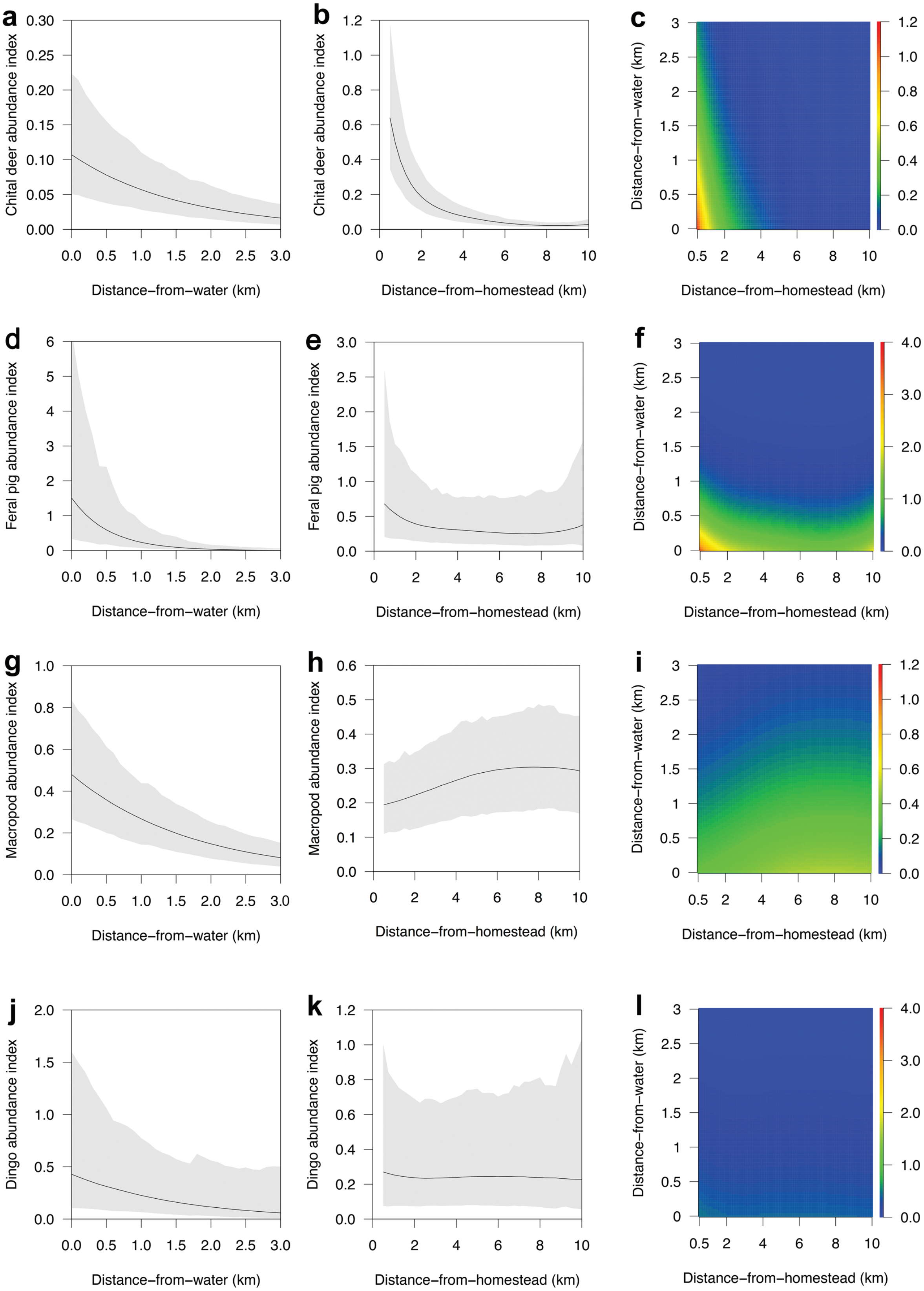

**Fig. 3.**—Relationships between the abundance index values of chital deer (*Axis axis*; a–c), feral pigs (*Sus scrofa*; d–f), macropods (g–i), and dingoes (*Canis dingo*; j–l), and distance from water (left column), distance from homestead (center column), and both variables (right column) at seven cattle ranches in North Queensland, Australia, in September–October 2015. The abundance index unit for chital deer and macropods is number of individuals per 24 hr per camera pair; for feral pigs and dingoes it is number of individuals per 7 days per camera pair. The mean distances from each of water and homestead were used for each camera pair. The maximum distances from a camera pair to the nearest water and homestead were 3.2 and 10.8 km, respectively. The nearest homestead was 225 m from a camera pair; hence, to avoid extrapolation the modeled relationship for this variable begins at 500 m.

**Table 3.**—Main taxa (≥ 3% frequency of occurrence [FO]) present in 127 dingo (*Canis dingo*) scats collected at Spyglass and Niall cattle ranches, North Queensland, Australia, in 2015 and 2016. Multiple taxa were detected in some scats. Taxa are listed in descending %FO.

| Taxon | *n* | %FO |
|---|---|---|
| Agile wallaby (*Notamacropus agilis*) | 64 | 50 |
| Chital deer (*Axis axis*) | 35 | 28 |
| Bird | 14 | 11 |
| European rabbit (*Oryctolagus cuniculus*) | 13 | 10 |
| Cattle (*Bos taurus*) | 9 | 7 |
| Feral pig (*Sus scrofa*) | 9 | 7 |
| Common wallaroo (*Osphranter robustus*) | 8 | 6 |
| Spectacled hare-wallaby (*Lagorchestes conspicillatus*) | 7 | 6 |
| Eastern gray kangaroo (*Macropus giganteus*) | 6 | 5 |
| Brushtail possum (*Trichosurus vulpecula*) | 4 | 3 |
| Rufous bettong (*Aepyprymnus rufescens*) | 4 | 3 |

but not that abundance was negatively affected by dingo abundance. Analysis of dingo scat contents revealed that Australia's top predator consumed chital deer at high frequencies (> 75%) near homesteads.

The most important determinant of the abundance of chital deer was distance from the nearest homestead, with negligible abundance > 4 km from homesteads. In contrast, distance from the nearest homestead was not an important predictor of the relative abundance of feral pigs, macropods, or dingoes. The most likely explanation for chital deer being most abundant near homesteads is the tendency for homesteads to be situated near higher-fertility river flats, where forage quality is higher (Watter et al. In press), and because homesteads are often associated with permanent natural or artificial water (e.g., at Felspar and Spyglass; Supplementary Fig. S2). The provision of supplementary forage and minerals for cattle around homesteads could benefit chital deer. Homesteads could also provide a "human shield" (sensu Berger 2007; Price et al. 2014) from dingo predation (see below). Whichever essential resources are inadvertently provided by human activity at homesteads, the strong association of chital deer with homesteads leads us to conclude that chital deer are "commensal" with humans in the NQDT.

Our camera study was conducted late in the dry season, when available water was restricted to artificial water points (i.e., dams and troughs), natural springs, and flowing or stagnant streams. The dependency of chital deer on water during the dry season has been reported in their native (Lydekker 1907; Dunbar Brander 1923; Schaller 1967) and invasive (Graf and Nichols 1966; Fuchs 1984) ranges. Six of the seven ranches in our study were using artificial dams and troughs to water their cattle, and there was evidence of these being used by chital deer during our study. Water was also a critical determinant of the relative abundance of feral pigs in our study area, supporting the contention that feral pigs are constrained by water availability in the dry season in semi-arid Australia (Choquenot and Ruscoe 2003). Feral pigs can tolerate high ambient temperatures only where both drinking water and dense vegetation suitable for shelter are available (Wilson et al. 1992; Choquenot et al. 1996). Macropods are marsupials that are considered analogous to small ungulates in size, ecology, and life history (Jarman 1991; Fisher et al. 2002). However, macropods have larger home range sizes and lower water requirements than ungulates (Munn et al. 2016; Lavery et al. 2018), and rainfall-related changes in food availability are considered to be more important for kangaroo abundances than water availability in Australia's rangelands (Lavery et al. 2018). In our study area, the two non-native ungulate species exhibited greater water dependency than the native macropods. The abundance of dingoes declined with increasing distance from water, consistent with the results of an analysis of track counts in arid central Australia (Brawata and Neeman 2011).

We considered the role of Australia's top mammalian predator in determining the abundance of chital deer—a factor that has been neglected in previous studies of Australia's non-native ungulates (Lundgren et al. 2018; Forsyth et al. 2019). A 4-fold increase in the relative abundance of invading sambar deer (*Cervus unicolor*) in southeastern Australia during 1984–2013 led to the occurrence of this species in dingo scats increasing from nil to 8% (Forsyth et al. 2018). In our study, the occurrence of chital deer in dingo scats was 75–100% within 1 km of homesteads, declining rapidly with increasing distance from homesteads; this pattern mirrors the trend in the relative abundance of chital deer observed in the camera study. There has been little work investigating how dingo diets are affected by local prey availability (Doherty et al. 2019), particularly for large introduced mammals (Forsyth et al. 2019), and this result illustrates how the diet of Australia's top terrestrial predator can vary over small distances according to the dependency of prey species on landscape features, as has been shown for apex mammalian predators on other continents (de Boer et al. 2010).

Given the large home range sizes of dingoes in northern Australia (Fleming et al. 2001), it is possible that chital deer and feral pigs were consumed well away from where scats containing these species were deposited. At a ranch ~200 km to the southwest of our study area, five GPS-tracked dingoes had home ranges of ≥ 62 km$^2$, but used smaller core areas of 5–23 km$^2$ with regular movements of > 20 km into sheep paddocks from nearby wooded areas (Allen et al. 2017). The gut transit times of dingoes have not, to our knowledge, been quantified, but for domestic dogs vary with fiber content and breed (Burrows et al. 1982; Hernot et al. 2005). For domestic breeds of similar body mass to dingoes, mean gut transit time was 33 hr for Standard Schnauzer and 35 hr for Labrador Retriever (Hernot et al. 2005). The strong relationships observed between the relative abundances of herbivores, their occurrences in scats, and distances to landscape features suggest that chital deer and feral pigs were eaten near where scats were deposited.

A limitation of the scat analysis is that it cannot readily determine whether chital deer were scavenged or killed by dingoes. It is likely that dingoes could kill healthy adult female chital deer, but would probably require multiple adults hunting cooperatively (Forsyth et al. 2019). In their native range, chital deer can form large groups to protect themselves from dholes (*Cuon alpinus*; 16–24 kg), which preferentially kill neonates (Venkataraman et al. 1995). Dingoes were subject to baiting at

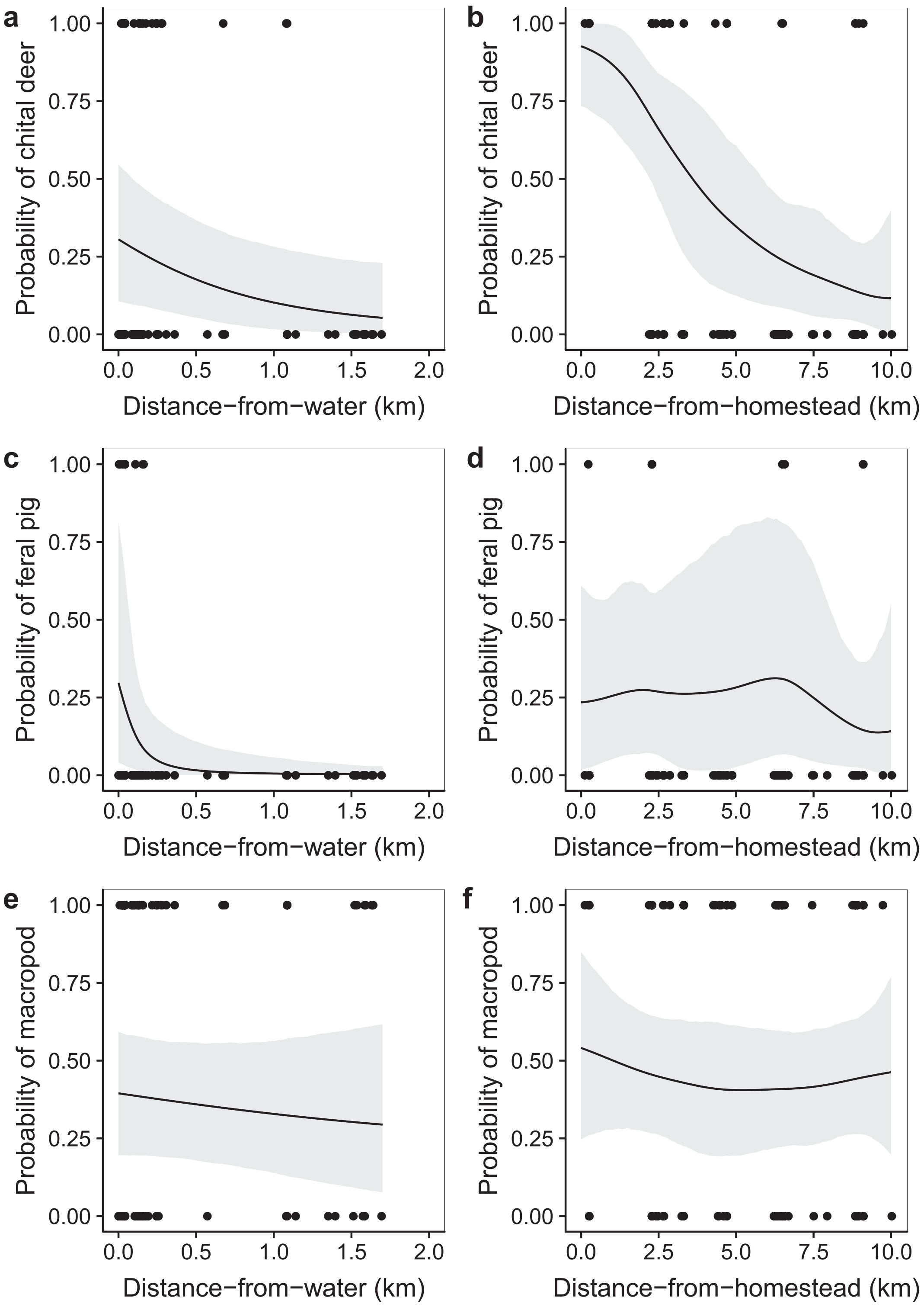

**Fig. 4.**—Effects of distance from water and distance from homestead on the probability of a dingo (*Canis dingo*) scat containing a, b) chital deer (*Axis axis*) (upper row); c, d) feral pig (*Sus scrofa*) (middle row); or e, f) macropod (lower row) at Spyglass and Niall cattle ranches, North Queensland, Australia, in September–October 2015 and November 2016. Solid lines are predicted mean probabilities, and shaded areas are 95% highest density credible intervals. Closed circles at $P = 1.00$ indicate a scat containing that taxa. Note that one scat could contain multiple taxa.

all seven ranches, and hence densities were likely lower than they would have been in the absence of these control activities. We also suspect that dingoes living around homesteads are more likely to be controlled by the ranchers than those living away from homesteads. There was no relationship between dingo abundance and distance from homesteads, but abundance data were sparse for this species compared with chital deer. Hence, the relationship between dingo abundance

**Table 4.**—Parameter estimates (all on the logit-scale) for the binomial models of chital deer (*Axis axis*), feral pig (*Sus scrofa*), and macropod occurrence in dingo (*Canis dingo*) scats collected at Spyglass and Niall cattle ranches, North Queensland, Australia, in 2015 and 2016. Distance from homestead was included as a predictor variable using a thin-plate regression spline, but has too many parameters to include here; see the modeled relationships in Fig. 4. The medians and lower and upper bounds come from the 95% high-density credible intervals for the posterior distributions.

| Taxon | Parameter | 2.5% | Median | 97.5% |
|---|---|---|---|---|
| Chital deer | Intercept | –1.31 | –0.54 | 0.19 |
| | Ranch – Spyglass | –1.50 | –0.44 | 0.63 |
| | Distance from water | –3.11 | –1.46 | –0.20 |
| Feral pig | Intercept | –2.56 | –1.26 | 0.09 |
| | Ranch – Spyglass | –3.47 | –1.37 | 0.33 |
| | Distance from water | –26.51 | –8.71 | –1.17 |
| Macropod | Intercept | –0.94 | –0.29 | 0.29 |
| | Ranch – Spyglass | 0.79 | 1.66 | 2.60 |
| | Distance from water | –1.15 | –0.32 | 0.56 |

and distance from homesteads had greater uncertainty than for chital deer (Fig. 3). It would be useful to experimentally evaluate the cessation of dingo control on dingo abundance, and particularly on the relationship between dingo abundance and homesteads, in our study area, but there would be substantial social barriers to doing this. Despite the absence of direct evidence in our study, it is possible that homesteads contribute to the persistence of chital deer in the NQDT by providing a human shield from dingoes (sensu Berger 2007; Price et al. 2014), as suggested by Roff (1960) and reported in parts of their native range (Geist 1998).

Water points have been identified as invasion hubs for cane toads (*Rhinella marina*) and feral goats in arid and semi-arid Australia (Letnic et al. 2014, 2015). Our study revealed the importance of water sources for chital deer and feral pigs during the hot dry season in Australia's dry tropics. We propose that water sources act as invasion hubs for chital deer and feral pigs by enabling them to survive annual dry periods and particularly long dry periods such as experienced during our study in 2015 (Fig. 2). In relatively wet years (e.g., 2012; Fig. 2), widespread natural water would likely help dispersing individuals survive and extend the invasion front. However, homesteads are at a lower density than water sources (< 10 km apart—James et al. 1999) throughout semi-arid and dry tropical Australia. They, too, are critical but less numerous invasion hubs for commensal chital deer. We predict that the spatial distribution of homesteads will be an important determinant of the rate and direction of any further range expansion of chital deer in northern Australia.

*Management implications.*—There is concern about the current and future impacts of invading chital deer in northern Australia (Jesser 2005), and in other non-native ranges such as Argentina (Gürtler et al. 2018) and Hawaii (Hess et al. 2015). Current control options are helicopter- and ground-based shooting (Hess et al. 2015; Gürtler et al. 2018; A. Pople et al., pers. obs.), and trapping (Pople et al. 2017). Our results suggest that the management of invasive chital deer populations can be optimized by conducting surveys (to detect extra-limital range expansions) and control activities (to reduce the abundance of established populations) at invasion hubs, i.e., within 4 km of homesteads and within 3 km of water during the hot dry season. Finally, the need for chital deer to drink daily during hot, dry conditions could be exploited in management programs, in particular by shooting from a hide and by trapping.

## Acknowledgments

This study was funded by Biosecurity Queensland. The authors declare no conflicts of interest. We thank all the ranchers who permitted us to work on their ranches, J. Hampton and H. Pople for helping collect dingo scats, and J. Birtles for editorial assistance. Comments from an anonymous reviewer, the Associate Editor, and Editor greatly improved the manuscript.

## Supplementary Data

**Supplementary Data SD1.**—Graphical depiction of camera trap spacings along each transect at the seven ranches.

**Supplementary Data SD2.**—Table of priors used in our Bayesian models.

**Supplementary Data SD3.**—Graphical depiction of the correlation between distance from homestead and distance from water for each of the seven ranches.

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*Submitted 7 January 2019. Accepted 18 August 2019.*

*Associate Editor was Jacob Goheen.*