



Short communication

Diurnal pattern of pre-weaning den visits and nursing in breeding pairs of captive dingoes (*Canis dingo*)Robyn Hudson^{a,*}, Heiko G. Rödel^b, Marise T. Elizalde^a, Gerard A. Kennedy^c, Bradley P. Smith^{d,*}^a Instituto de Investigaciones Biomédicas, Universidad Nacional Autónoma de México, Ciudad Universitaria, CP 04510, CDMX, Mexico^b Laboratoire d'Ethologie Expérimentale et Comparée EA4443, Université Paris 13, Sorbonne Paris Cité, Villetaneuse, France^c School of Health and Biomedical Sciences, College of Science, Engineering and Health, RMIT University, P.O. Box 71, Bundoora, Victoria, Australia^d Appleton Institute, Central Queensland University, 44 Greenhill Road, Wayville, South Australia 5034, Australia

ARTICLE INFO

Article history:

Received 30 January 2018

Accepted 3 July 2018

Available online 5 July 2018

Handled by Sabine Begall

Keywords:

Canis lupus
Den attendance
Parental care
Suckling
Wild dog

ABSTRACT

The period before pups are weaned represents a key developmental stage for canids that is directly related to the survivability of the pack. Yet our understanding of the role of the parents during this period when pups are confined to a den is rather limited. We sought further insight into this period by observing diurnal patterns of pre-weaning den visits and nursing behaviour in a captive population of dingoes (*Canis dingo*). We continuously video-monitored behaviour at dens of four captive, genetically pure, dingo pairs (one litter each) during the first three postpartum weeks just before the start of weaning. Mothers occupied the den almost continuously during the night, but significantly less so during the day, and consistently spent most den time nursing. Fathers were largely absent from inside the den despite lack of apparent aggression from females, low outside temperatures, and space for them inside. They spent a large percentage of time on top of the den, suggestive of sentinel duty, although further experiments are necessary to substantiate this. Although limited to captive animals, our observations are consistent with scant reports of bi-parental care in wild dingoes and with suggestions in the literature that reduced parental care in household and free-ranging domestic dogs might be, at least partly, due to the weakening of bi-parental care during their long history of close association with and dependence on humans.

© 2018 Deutsche Gesellschaft für Säugetierkunde. Published by Elsevier GmbH. All rights reserved.

There is still little detailed information on early parental care in canids, particularly during the pre-weaning period when the young are completely dependent on the mother's milk (Arteaga et al., 2013; Hudson et al., 2016). This is even the case for the grey wolf (*Canis lupus*), arguably the best studied of the wild canids in this regard (see Packard, 2003, and references therein). Most of what is known comes largely from anecdotal observations in the field, or from studies in captivity of both wild and domestic canids (Lord et al., 2013). The most notable gaps relating to parental care exist in relation to the presence of the male and female at den sites, nursing schedules, and the temporal organisation of parental behaviour across the 24-h day. This is understandable given that before the start of weaning at around four weeks of age the young are typically confined to an underground den, difficult for human observers to access and where disturbance might result in changes in the

behaviour of the parents and even in them relocating or abandoning the young (e.g., Thomson, 1992a; Smith and Vague, 2017).

Free-ranging domestic dogs appear to differ notably from wild canids in relation to characteristics and frequency of reproductive activity (e.g., less marked seasonality, earlier age of first reproduction, greater frequency of oestrus, less marked pair bonding) and parental feeding (e.g., poor nursing, failure of male or other pack members to provision the mother and young) (Boitani et al., 1995; review by Lord et al., 2013). These differences are thought to reflect the domestic dog's adaptation to the human niche, and ready access to associated resources relaxing the selection pressure for extended and biparental care. Investigating the patterns and function of parental care across canid species (or subspecies) may help identify commonalities across the genus and provide insight into the impact of domestication and feralisation on parental care. Comparative information on early parent-young relations is fundamental to developing a fuller understanding of canid biology (Lord et al., 2013), as well as of the reproductive success of pairs and packs (Benson et al., 2013; Fuller et al., 2003). In turn, knowledge of parental care can assist in the conservation and captive manage-

* Corresponding authors.

E-mail addresses: rhudson@biomedicas.unam.mx (R. Hudson), b.p.smith@cqu.edu.au (B.P. Smith).

ment of wild canids (Smith and Watson, 2015), and provide insight into the influence of domestication on canid parental behaviour.

With the aim of extending our knowledge of parental care during the pre-weaning period in the genus *Canis*, we focus here on the dingo (*Canis dingo* – but also referred to as *Canis lupus dingo*, *Canis familiaris dingo* or simply as *Canis familiaris*; Crowther et al., 2014; Jackson et al., 2017), a free-ranging canid endemic to Australia (Smith, 2015a). The dingo provides a unique comparative opportunity to investigate the impact of domestication on dog evolution under natural selection. Although sharing a genetic lineage with dogs (Ardalan et al., 2012; Oskarsson et al., 2011; Sacks et al., 2013; Savolainen et al., 2004), the dingo has been a wild-living canid on a continent geographically isolated from other canids (including dog or wolf lineages), and independent from humans for at least 5000 years until the arrival of the British and their dogs in 1788 (Cairns and Wilton, 2016; Cairns et al., 2017; Smith and Litchfield, 2009; Smith, 2015a). Reports directly relating to dingo reproductive, parental and denning behaviour are scant, with most restricted to anecdotal observations (e.g., Corbett and Newsome, 1975; Harden, 1981; Jones and Stevens, 1988; Thomson, 1992a; Smith and Vague, 2017), or conducted with captive populations (e.g., Breckwoldt, 1988; Corbett, 1988; Hudson et al., 2016).

Like most wild canids (Lord et al., 2013), male and female dingoes exhibit long-term pair bonding, maintain and defend a shared territory, cooperatively care for the young, and reproduce seasonally (Corbett and Newsome, 1975; Thomson, 1992a,b,c; Corbett, 2001; Lord et al., 2013; Smith, 2015a). Dingo pups are generally born in dens in the winter months (June to August), which coincides with the period best suited for rearing young (Smith, 2015b). Litter size varies according to seasonal conditions and with the condition and past experience of the mother. The average litter size is four to five pups, with a possible range of one to 10 (Catling et al., 1992; Corbett and Newsome, 1975; Corbett, 2001; Jones and Stevens, 1988). Choice of den sites is generally similar to that of other wild canids – including preference for elevated sites providing extensive views of lower approaches, close to water, and with the den opening positioned so as to offer maximum protection from the weather. Site selection varies according to food resources and habitat, and can include hollow logs, enlarged rabbit warrens, rock piles, or under trees or tussocks (Smith and Vague, 2017; Thomson, 1992a). Alloparental behaviour has been identified in both wild (Corbett and Newsome, 1975; Corbett, 2001; Thomson, 1992a) and captive dingoes (Corbett, 1988), beginning at 15 days postpartum (Breckwoldt, 1988). Communal denning has also been observed in locations where resources are abundant (Smith and Vague, 2017). However, it is clear that specific parental behaviours (e.g., the role of the father, diurnal patterns of care) are not well understood for most wild canids including the dingo (see Lord et al., 2013), and particularly during the first three postnatal weeks, which occur underground and so out of human sight.

In this paper we describe the pattern of parental care in reproductive pairs of captive dingoes based on continuous 24-h monitoring of the behaviour of parents and pups within the den during the first three postnatal weeks, that is, just before the start of weaning. Although our study has the limitation of being conducted with captive animals kept in single pairs, the results might provide a useful starting point for further work under the hugely more difficult conditions in nature. We expected dingoes' pattern of early parental care to reflect that observed in wild canids (e.g. wolves) given their long separation from cohabitation with humans and similarity to wild canids in other aspects of reproduction rather than to dogs (reviewed by Lord et al., 2013). Specifically, we expected greater participation of fathers as reflected by greater den attendance than appears to be the case in free-ranging domestic dogs.

Methods have been published in detail in a previous study (Hudson et al., 2016) from which the present, completely new data are drawn. Four pairs of dingoes and their litters, born in May/June 2013, contributed to the study (Table 1). Parents were captive born from wild-caught animals and raised at the Dingo Discovery Centre (–37.565184 S, 144.566024 E), a private facility located in Victoria, Australia, where the present study was conducted. All wild-caught animals had passed an analysis of genetic purity conducted by the University of New South Wales, Australia (Wilton, 2001). The breeding pairs were housed in pens (9 × 1.5 m = 13.5 m²) comprising 10.5 m² of gravel flooring and 3 m² of concrete flooring where a wooden den box (94 × 63.5 × 86 (high) cm, with a 36 × 46 cm opening at the top of the long side) was located (Fig. 1; see video clip in Supplementary material). Shredded paper was placed inside the den and was replaced daily or as required. Once the pups were able to walk and to independently leave the den (at approximately 20 days of age) the box was inverted so they could readily leave it. A corrugated iron roof covered 2 m of the pen above the concrete section, and the remaining roof was covered with wire mesh to prevent escape. The walls of the pens were 2 m high, of wire mesh, with the addition of 1.2 m high floor-level sheets of corrugated iron to act as windbreaks and to prevent fighting between neighbours. Observations were made from May to June 2013 during the Southern Hemisphere winter, which is the normal, once-yearly breeding period for dingoes (Lord et al., 2013; Smith, 2015b).

The parents were accustomed to human presence and handling and appeared well adjusted to the study conditions. In general, adult dingoes were fed a combination of dry dog food and fresh chicken (carcass or ground carcass mince) each morning (between 0900 and 1200 h). However, starting 14 days before whelping, the mothers were also fed in the evening (between 1600 and 1800 h). This continued until the pups started to leave the den at approximately 21 days of age and to eat semi-solid food, by which time their teeth had fully erupted. The pens and dens were also cleaned daily during the morning feed. The evening feed marked the time when human activity in the vicinity of the dingo facility ceased for the day. During the study period direct contact with the animals was restricted to two regular members of staff. This included handling the pups for health checks and weighing (Crofton kitchen scales, limit 4 kg, resolution 1 g) at birth and then on average every third day (see Table 1 for birth weights). Visits to the sanctuary were restricted until the pups had been weaned and transferred to communal enclosures for juveniles. For further details on the management of dingoes at the sanctuary see Smith and Watson (2015).

Behaviour within the dens was recorded continuously using a small day/night surveillance camera (1/3" SwannTruColor image sensor, 728 × 488 pixels; Swann Pro 530, Swann Communications) that provided a good overview of the interior (Fig. 1a, b), and a digital video recorder (Swann 4 channel DVR, model DVR4-4000, Swann Communications). Recordings were made at a frame rate of 20 fps, and a maximum bit rate of 1024 kbps, in colour during the day and switched to black and white at night using infra-red LED (minimum illumination 0 lx with infra red activated). The cameras were installed in a top corner of each of the four dens at least 24 h prior to birth. Recording began at this time and ceased when the pups started to leave the den, or at 21 days, whatever occurred first. For behavioural analysis we used the two most complete 24-h records per week (i.e., six 24-h records for each parental pair). This selection was necessary due to lost footage from power outages and destruction of cameras by the dingoes, and resulted in a total sample of 576 h of observation. The main behaviours scored were the frequency and time spent by each parent in the den and the time mothers spent nursing. This was defined as the time during which at least one pup was attached to a nipple but without implying milk ingestion. Behaviours were scored per second but for the analyses

Table 1

Details of the parents and litters of this study. Birth weights were taken within 48 h of birth. Parents were born at the Dingo Discovery Centre from genetically pure wild-caught animals.

Mother	Age (years)	Parity	Father	Date of birth	Litter size	Sex		Weight at birth (g)	Natal deaths	Post natal deaths	Final litter size
						M	F				
Amelia	2	0	Wallace	9-5-13	5	2	3	M: 344, 331 F: 324, 311, 288	0	0	5
Petal	5	0	Bingo	17-5-13	6	4	2	M: 358, 350, 322, 310, F: 334, 292	0	0	6
Freckle	8	2	Sterling	24-5-13	6	2	4	M: 368, 311 F: 366, 360, 337, 250 ^a	0	1 ^a	5
Opal	7	3	Teddy	1-6-13	7	3	2	M: 391, 391, 375, 356 ^b F: 304, 284	0	2 ^b	5

^a On day 3 one pup went missing. Cause unknown.

^b Two dingo pups euthanized by DDC staff at birth. The details of the second euthanized pup are unknown.



Fig. 1. View inside a den box with a nursing mother during the first (a) and third (b) postnatal week, and of the dingo enclosure with the father on top of the den (c). Images are screen shots taken from actual footage.

(see below) data were collapsed into 1-hour bins (see Supplementary material for a video clip of the behaviour of a mother and her week-old pups in the den).

External ambient air temperature and temperature in the den were continuously monitored and recorded in 5 min intervals using temperature data loggers (HOBO Pendant® Temperature/Alarm Data Logger 64K, model UA-001-64; measurement range −20 to 70°C; resolution 0.14°C at 25°C). Loggers were attached to the ceiling of the far left corner of the den away from the entrance, and to the outside of the den at the same height on the side closest to the enclosure wall. During the study period the temperature outside the dens during the day (0700–1800 h) was mean 13.03°C, 0.06 SE, range 6.06–24.64, and during the night (1800–0700 h) was mean 11.26°C, 0.05 SE, range 5.96–22.33. The temperature inside the dens during the light phase was mean 14.50°C, 0.06 SE, range 6.98–26.19, and during the dark phase was mean 12.64°C, 0.05 SE, range 6.98–23.87. Wilcoxon signed-rank tests reported that during both the day and night, temperatures inside the dens were significantly higher than external temperatures ($Z = -47.78$, $P < 0.001$) and $Z = -49.65$, $P < 0.001$, respectively).

Mothers gave birth with no natal deaths, raised their young to weaning without apparent difficulty, and allowed observation and manipulation of their pups by sanctuary staff without protest. After weaning at around 10–12 weeks of age pups were sold as pets or to zoos or fauna parks. Methods were approved by the Central Queensland University Animal Ethics Committee, project number A12/11-293.

Statistical analyses were done with R, version 3.3.2 (R Core Team, 2016). We applied generalized linear mixed-effects models (GLMM) for proportional data, using a model structure for binomial distribution with a logit link. Thus, for analysis, the different response variables (mother's presence in den in min/h and mother's nursing activity in % time) were transformed into proportions. Calculations were based on Laplacian maximum likelihood estimates

using the package *lme4* (Bates et al., 2015). P -values were calculated by Wald Chi-square tests. Analyses were based on repeated measurements of the four parental pairs across the first three postpartum weeks, with two full days of sampling per week and pair (see above for details). Data were analyzed on an hourly basis, either as min/h (for the response variables 'time spent by mothers in the den' and 'time spent by fathers in the den') or as % observation time (for the response variable '% time in the den mothers spent nursing').

For each of the three response variables given above we ran a statistical model considering week as a factor with three levels and photoperiod as a factor with two levels (day and night). The daily photoperiod was determined based on the start and end of civil twilight at the study site (Melbourne, Australia) during early May to early June 2013 using information available at www.timeanddate.com/sun. Based on averages across the observation days, the start of daylight was defined as 0655 h and the start of night as 1738 h. To account for repeated measurements we included the identity of the parental pair and the postpartum day of sampling as random factors. We also included an observation-level random factor to account for over-dispersion of our models (Browne et al., 2005).

Mothers spent on average 1131.2 min per 24 h period (± 19.5 SE) in the den during the first three postpartum weeks; significantly more and around 10-fold the mean time fathers spent in the den (values for fathers see below; $\chi^2_1 = 291.53$, $P < 0.001$). Mothers' time in the den showed a clear diurnal pattern; whereas they remained almost continuously in the den during the night they spent significantly less time there during the day ($\chi^2_1 = 439.31$, $P < 0.001$; Fig. 2a–c). The time they spent in the den during the night did not differ significantly between weeks 1, 2 and 3 ($P > 0.30$ for all pairwise comparisons), but during the day mothers spent significantly more time in the den during the first postpartum week (mean 40.2 min/h ± 1.9 SE) compared to the second week (mean 32.1 min/h ± 2.2 SE; $\chi^2_1 = 8.73$, $P = 0.003$), and to the third week (mean 26.5 min/h

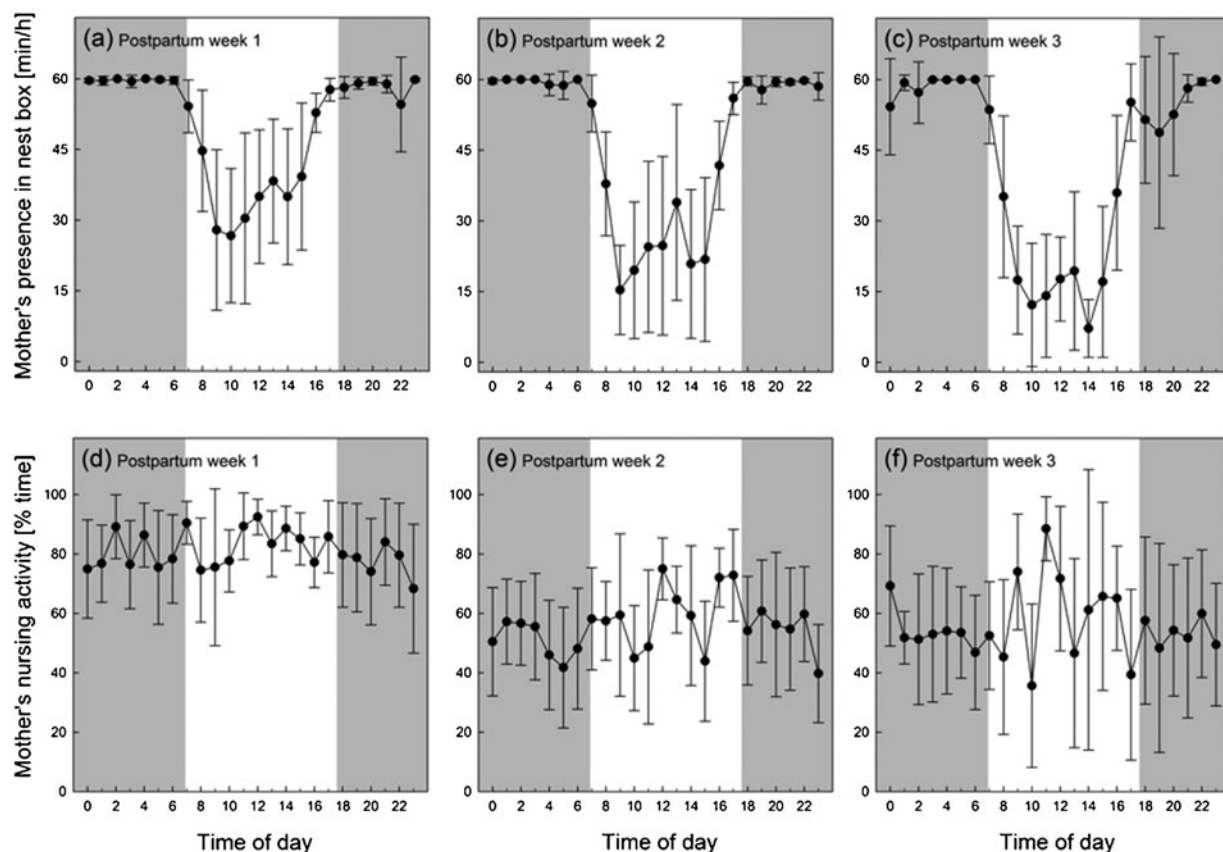


Fig. 2. Pattern across the day of mothers' presence in the den (a–c) and percentage time mothers spent nursing while in the den (d–f) during postpartum weeks 1–3. Mean values (with 95% confidence intervals) represent data from two 24-h periods per week from four mothers. Night-time indicated by grey shading. Time of day is given in hours with 0 representing the time from 0001–0100 h, and 23 the time from 2301 to 2400 h. See text for statistics.

± 2.4 SE; $\chi^2_1 = 19.85$, $P < 0.001$), but with no statistically significant difference between weeks 2 and 3 ($\chi^2_1 = 3.12$, $P = 0.07$).

The most notable finding was the large amount of time mothers spent in the den, although markedly less so during the day. The most obvious explanation for this difference was the possible effect of human activity in or around the pens during the day, particularly during the morning hours when the initial sharp drop in the time mothers spent in the den coincided with feeding and pen and den cleaning. Although this schedule of maintenance is surely different to the pattern of feeding and other daily activities of dingoes in the wild, reports suggest them to be very flexible in their feeding habits and diet, and when unmolested, tolerant of close human presence (Thomson, 1992b; Smith and Vague, 2017). From the early afternoon, mothers then spent increasing time back in the den (Fig. 2a–c). A contributing factor to greater night-time den occupancy might also have been mothers seeking shelter from the cold.

When in the den, mothers spent a large percentage of time 'nursing' irrespective of time of day (Fig. 2d–f). As we reported previously (Hudson et al., 2016) this did not necessarily involve the whole litter simultaneously, and it was common for one or two pups to be attached to a nipple while others played or 'slept'. No diurnal pattern in mothers' nursing behaviour was apparent, and the percentage time while in the den they spent nursing at least one pup did not differ significantly between day and night ($\chi^2_1 = 0.35$, $P = 0.55$; Fig. 2d–f). There were, however, significant differences between postpartum weeks 1, 2 and 3 ($\chi^2_1 = 23.27$, $P < 0.001$). Post hoc comparisons showed that the percentage time mothers spent nursing was significantly greater during the first postpartum week (mean $80.8\% \pm 1.3$ SE) than during the second week (mean $55.7\% \pm$

1.6 SE; $\chi^2_1 = 13.98$, $P < 0.001$) and third week (mean $55.6\% \pm 2.0$ SE; $\chi^2_1 = 12.04$, $P < 0.001$), whilst the percentage time spent nursing during postpartum weeks 2 and 3 did not differ significantly ($\chi^2_1 = 0.03$, $P = 0.86$).

Fathers spent relatively little time in the den, on average only 106.1 min per 24-hour period (± 17.2 SE) during the first three postpartum weeks, although there appeared to be sufficient room. Based on the admittedly small available sample size, the average time did not differ significantly across the first three postnatal weeks, although there was an increase in the mean values (week 1: mean 1.7 min. h ± 0.7 SE; week 2: mean 3.0 min. h ± 1.0 SE; week 3: mean 9.0 min. h ± 1.8 SE; $\chi^2_2 = 2.69$, $P = 0.26$). There were also no statistically significant differences in the time fathers spent in the den at night (mean 7.2 min/h ± 1.3 SE) and during the day (mean 1.1 min/h ± 0.3 SE; $\chi^2_1 = 2.51$, $P = 0.11$).

The reasons for paternal absence are not clear. No overt aggression by females towards their mate in or at the den was seen, and the den was sufficiently large to accommodate both parents. However, such behaviour may not be uncommon among males during the pre-weaning period. Packard (2003), and references therein) suggests that in grey wolves the contribution of the father consists mainly in defence of the home site (particularly from predators, in the case of dingoes potentially wedge-tailed eagles (*Aquila audax*), cattle or buffalo, snakes, and goannas; Fleming et al., 2001), and hunting and provisioning the lactating female. During the second month, and thus beyond the scope of the present study, this changes, with male wolves spending almost as much time in the den as the mother (Packard, 2003).

In the present study the males spent considerable time on top of the den (Fig. 1c). A simple explanation might be that this position

was the most comfortable in the enclosure. However, we suggest that the males were possibly acting as 'sentinels' and adopting a protective role enabling their mate to remain calmly within the den with the pups. This is consistent with anecdotal reports of male and female grey wolves residing by den entrances, seemingly acting as sentinels (e.g. Murie, 1944; Packard, 2003). Also, in descriptions of the dens of wild dingoes, Thomson (1992a) and Smith and Vague (2017) report a preference for elevated sites, which include extensive views of lower approaches, and with well-worn rest pads near the entrance. To check this sentinel hypothesis it would be useful to have information on dingoes' resting behaviour in relation to the den during winter but no longer with pups present.

Despite the limitations of studying captive animals our results seem robust. Behavioural patterns were consistent across the four breeding pairs – all first generation descendants of wild-caught, genetically pure dingoes – and despite differences in parents' age and parity. The results are also consistent with observations of den attendance and parental behaviour in the taxonomically closely related grey wolf (Mech and Boitani, 2003; Mech et al., 1999). Clearly, the validity of these results needs to be checked against further information on the parental behaviour of dingoes in the wild. The results nevertheless provide a starting point for a comparison with parental behaviour in other canid species, and particularly with free-ranging dogs (cf. Arteaga et al., 2013; Hudson et al., 2016). It is possible that in dogs the lack of a close pair bond and clear division of labour at the den is one reason for their generally reduced breeding performance and the inability of free-ranging packs to form self-sustaining populations independent of human habitation (Boitani et al., 1995).

Conflict of interest

None.

Acknowledgements

We thank Lyn Watson and Lyn Whitworth from the Dingo Discovery Centre and Carolina Rojas for technical and bibliographical assistance. Financial support was provided by Central Queensland University, the Australian Dingo Foundation, and by the French-Mexican scientific exchange program ECOS Nord - CONACYT (M14A02). This study was part of the master's thesis of M.T.E who received a post-graduate fellowship (294591) from the Mexican national funding agency CONACYT.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.mambio.2018.07.002>.

References

- Ardalan, A., Oskarsson, M., Natanaelsson, C., Wilton, A., Ahmadian, A., Savolainen, P., 2012. Narrow genetic basis for the Australian dingo confirmed through analysis of paternal ancestry. *Genetica* 140, 65–73, <http://dx.doi.org/10.1007/s10709-012-9658-5>.
- Arteaga, L., Rödel, H.G., Trejo Elizalde, M., González, D., Hudson, R., 2013. The pattern of nipple use before weaning among littermates of the domestic dog. *Ethology* 119, 12–19, <http://dx.doi.org/10.1111/eth.12030>.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. *Fitting linear mixed-effects models using lme4*. *J. Stat. Software* 67, 1–48.
- Benson, J.F., Mills, K.J., Loveless, K.M., Patterson, B.R., 2013. Genetic and environmental influences on pup mortality risk in a *Canis* hybrid zone. *Biol. Conserv.* 166, 133–141, <http://dx.doi.org/10.1016/j.biocon.2013.06.018>.
- Boitani, L., Francisci, F., Andreoli, G., 1995. *Population biology and ecology of feral dogs in central Italy*. In: Serpell, J.A. (Ed.), *The Domestic Dog: Its Evolution, Behaviour and Interactions with People*. Cambridge University Press, Cambridge, pp. 218–244.
- Breckwoldt, R., 1988. *A Very Elegant Animal: The Dingo*. Angus and Robertson, Melbourne.
- Browne, W.J., Subramanian, S.V., Jones, K., Goldstein, H., 2005. Variance partitioning in multilevel logistic models that exhibit overdispersion. *J. R. Stat. Soc. Ser. A* 168, 599–613, <http://dx.doi.org/10.1111/j.1467-985X.2004.00365.x>.
- Cairns, K.M., Wilton, A.N., 2016. New insights on the history of canids in Oceania based on mitochondrial and nuclear data. *Genetica* 144, 553–565, <http://dx.doi.org/10.1007/s10709-016-9924-z>.
- Cairns, K.M., Brown, S.K., Sacks, B.N., Ballard, J.W.O., 2017. Conservation implications for dingoes from the maternal and paternal genome: multiple populations, dog introgression, and demography. *Ecol. Evol.* 7, 9787–9807, <http://dx.doi.org/10.1002/ece3.3487>.
- Catling, P., Corbett, L.K., Newsome, A., 1992. Reproduction in captive and wild dingoes (*Canis familiaris* dingo) in temperate and arid environments of Australia. *Wildl. Res.* 19, 195–209, <http://dx.doi.org/10.1071/WR9920195>.
- Corbett, L.K., 1988. Social dynamics of a captive dingo pack: population regulation by dominant female infanticide. *Ethology* 78, 177–198, <http://dx.doi.org/10.1111/j.1439-0310.1988.tb00229.x>.
- Corbett, L.K., 2001. *The Dingo in Australia and Asia*, 2nd edn. JB Books, Adelaide.
- Corbett, L., Newsome, A.E., 1975. Dingo society and its maintenance: a preliminary analysis. In: Fox, M.W. (Ed.), *The Wild Canids: Their Systematics, Behavioral Ecology and Evolution*. Van Nostrand-Reinhold, New York, pp. 369–379.
- Crowther, M.S., Fillios, M., Coleman, N., Letnic, M., 2014. An updated description of the Australian dingo (*Canis dingo* Meyer, 1793). *J. Zool.* 293, 192–203, <http://dx.doi.org/10.1111/jzo.12134>.
- Fleming, P., Corbett, L., Harden, R., Thomson, P.C., 2001. *Managing the Impacts of Dingoes and Other Wild Dogs*. Bureau of Rural Sciences, Canberra, ISBN 0642704945.
- Fuller, T.K., Mech, L.D., Cochrane, J.F., 2003. *Wolf population dynamics*. In: Mech, L.D., Boitani, L. (Eds.), *Wolves: Behavior, Ecology, and Conservation*. University of Chicago Press, Chicago & London, pp. 161–191.
- Harden, R., 1981. A look at the dingo. *Aust. Nat. Hist.* 20, 191–194.
- Hudson, R., Rödel, H.G., Trejo Elizalde, M., Arteaga, L., Kennedy, G.A., Smith, B.P., 2016. Pattern of nipple use by puppies: a comparison of the dingo (*Canis dingo*) and the domestic dog (*Canis familiaris*). *J. Comp. Psychol.* 130, 269–277, <http://dx.doi.org/10.1037/com0000023>.
- Jackson, S.M., Groves, C.P., Flemming, P.J., Aplin, K.P., Eldridge, M.D., Gonzales, A., et al., 2017. The wayward dog: is the Australian native dog or dingo a distinct species? *Zootaxa* 431, 201–224, <http://dx.doi.org/10.11646/zootaxa.4317.2.1>.
- Jones, E., Stevens, P.L., 1988. Reproduction in wild canids, *Canis familiaris*, in the eastern highlands of Victoria. *Wildl. Res.* 15, 385–394, <http://dx.doi.org/10.1071/WR9880385>.
- Lord, K., Feinstein, M., Smith, B.P., Coppinger, R., 2013. Variation in reproductive traits of members of the genus *Canis* with special attention to the domestic dog (*Canis familiaris*). *Behav. Proc.* 92, 131–142, <http://dx.doi.org/10.1016/j.beproc.2012.10.009>.
- Mech, L.D., Boitani, L., 2003. *Wolves: Behavior*. In: *Ecology and Conservation*. The University of Chicago Press, Chicago & London.
- Mech, L.D., Wolf, P.C., Packard, J.M., 1999. Regurgitative food transfer among wild wolves. *Can. J. Zool.* 77, 1192–1195, <http://dx.doi.org/10.1139/z99-097>.
- Murie, A., 1944. *The wolves of Mount McKinley*. In: National Park Service, *Fauna Series No. 5*. US Government Printing Office, Washington, DC.
- Oskarsson, M.C.R., Klütsch, C.F.C., Boonyaparakob, U., Wilton, A., Tanabe, Y., Savolainen, P., 2011. Mitochondrial DNA data indicate an introduction through Mainland Southeast Asia for Australian dingoes and Polynesian domestic dogs. *Proc. R. Soc. Lond. Ser. B-Biol. Sci.* 279, 967–974.
- Packard, J.M., 2003. Wolf behavior: reproductive, social and intelligent. In: Mech, L.D., Boitani, L. (Eds.), *Wolves: Behavior, Ecology, and Conservation*. University of Chicago Press, Chicago & London, pp. 35–65.
- R Core Team, 2016. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna www.R-project.org.
- Sacks, B.N., Brown, S.K., Stephens, D., Pedersen, N.C., Wu, J.-T., Berry, O., 2013. Y Chromosome analysis of dingoes and Southeast Asian village dogs suggests a Neolithic continental expansion from Southeast Asia followed by multiple Austronesian dispersals. *Mol. Biol. Evol.* 30, 1103–1118, <http://dx.doi.org/10.1093/molbev/mst027>.
- Savolainen, P., Leitner, T., Wilton, A.N., Matisoo-Smith, E., Lundeberg, J., 2004. A detailed picture of the origin of the Australian dingo, obtained from the study of mitochondrial DNA. *Proc. Nat. Acad. Sci.* 101, 12387–12390, <http://dx.doi.org/10.1073/pnas.0401814101>.
- Smith, B.P., 2015a. *The Dingo Debate: Origins*. In: *Behaviour and Conservation*. CSIRO Publishing, Melbourne.
- Smith, B.P., 2015b. *Biology and behaviour of the dingo*. In: Smith, B.P. (Ed.), *The Dingo Debate: Origins, Behaviour and Conservation*. CSIRO Publishing, Melbourne, pp. 25–53.
- Smith, B.P., Litchfield, C.A., 2009. A review of the relationship between indigenous Australians, dingoes (*Canis dingo*) and domestic dogs (*Canis familiaris*). *Anthrozoös* 22, 111–128, <http://dx.doi.org/10.2752/175303709X434149>.
- Smith, B.P., Vague, A.-L., 2017. The denning behaviour of dingoes (*Canis dingo*) living in a human-modified environment. *Aust. Mammal.* 39, 161–168, <http://dx.doi.org/10.1071/AM16027>.
- Smith, B.P., Watson, L., 2015. The role of private sanctuaries in dingo conservation and the management of dingoes in captivity. In: Smith, B.P. (Ed.), *The Dingo Debate: Origins, Behaviour and Conservation*. CSIRO Publishing, Melbourne, pp. 277–299.

- Thomson, P.C., 1992a. The behavioural ecology of dingoes in North-western Australia: II. Activity patterns, breeding season, and pup rearing. *Aust. Wildl. Res.* 19, 519–530, <http://dx.doi.org/10.1071/WR9920519>.
- Thomson, P.C., 1992b. The behavioural ecology of dingoes in North-western Australia: III. Hunting and feeding behaviour, and diet. *Aust. Wildl. Res.* 19, 531–541, <http://dx.doi.org/10.1071/WR9920531>.
- Thomson, P.C., 1992c. The behavioural ecology of dingoes in North-western Australia: IV. Social and spatial organisation, and movements. *Aust. Wildl. Res.* 19, 543–563, <http://dx.doi.org/10.1071/WR9920543>.
- Wilton, A., 2001. DNA methods of assessing dingo purity. In: Dickman, C.R., Lunney, D. (Eds.), *A Symposium on the Dingo*. Royal Zoological Society of New South Wales, Sydney, pp. 49–56.