

Do female dingo–dog hybrids breed like dingoes or dogs?

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Abstract. Hybridisation between animals that breed once (e.g. dingoes) and twice (e.g. domestic dogs) annually may produce offspring that breed either way. This question was investigated by determining the breeding seasonality of female dingo–dog hybrids in south-east Queensland, Australia, through evaluating macroscopic and histological features of 71 female reproductive tracts. All animals were sourced from urban areas where levels of hybridisation are generally high. Most animals trapped in summer were pups less than 6 months of age. A peak of uterus diameter and weight coincided with a peak of *corpus luteum* in winter. The follicular phase was characterised by growing follicles, ~1–3 mm wide, in late summer and autumn. Only two of the animals (1.4%) showed out-of-season reproductive cycles: one was found with *corpus luteum* in summer and another in autumn. Our data clearly show that hybrids have a single annual breeding season in winter, exhibiting the same breeding seasonality as dingoes. Our findings are similar to those found in the New Guinea singing dog. Future studies should be conducted to understand and exploit the mechanism and drivers of the breeding seasonality of dingo–dog hybrids to develop more effective management of their populations.

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Introduction

The dingo (*Canis familiaris*) is an ancient breed of domestic dog thought to have evolved from Asiatic wolves (Claridge *et al.* 2014). Dingoes were introduced in Australia ~5000 years ago, probably by seafarers (Fleming *et al.* 2012; Claridge *et al.* 2014). European settlement brought modern domestic dogs (*Canis familiaris*) to the continent and subsequent breeding with dingoes has resulted in dingo–domestic dog hybrids. Dingoes, domestic dogs, and hybrids between the two are collectively known as ‘wild dogs’. The introgression of modern domestic dog genetics into dingo populations has occurred across much of mainland Australia, resulting in a high prevalence of hybrids in the more populated south and eastern regions (Stephens *et al.* 2015). For example, recent studies have reported that 90% of wild dogs in south-east Queensland are hybrids, although most remain much more genetically similar to dingoes than domestic dogs (Elledge *et al.* 2008; Stephens *et al.* 2015; M. Gentle, unpubl. data).

Dingoes are considered a top predator in Australia and their importance as biodiversity regulators is advocated but remains controversial (Glen and Dickman 2005; Letnic *et al.* 2012; Allen *et al.* 2013a). However, dingo-hybrids residing around urban areas can be a threat to people, their livestock and pets (Allen *et al.*

2013b). Hybrids are also listed as a key threatening process to dingoes (Major 2009) given that the continuing transition from dingoes to dingo–dog hybrids across Australia threatens the persistence of dingoes as a distinct breed of conservation value (Corbett 2008). Even though the ecology and control of dingoes and hybrids are well studied (reviewed by Corbett 2001; Purcell 2010; Smith 2015), there is a paucity of knowledge of their reproductive biology, with only four published research papers (i.e. Catling 1979; Jones and Stevens 1988; Catling *et al.* 1992; Woodall *et al.* 1993) and some communications (Green and Catling 1977; Thomson 1992; Fleming *et al.* 2001; Purcell 2010; Smith 2015). This is concerning given the potential value of reproductive information to both control and conservation programs.

Previous studies have reported that female dingoes show a monoestrous cycle with one breeding season per year in temperate and arid climates (Jones and Stevens 1988; Catling *et al.* 1992). The breeding season commences in February (late summer) and continues up to June (early winter) (Corbett 2001). The whelping season occurs in winter between June and August, followed by rearing in spring and early summer (September to November) (Corbett 2001). It is likely that the breeding season in dingoes is

triggered by changes in the duration of daylight (Smith 2015). Pure male dingoes from central arid Australia show the same seasonality, with semen being produced only during the breeding season. However, non-seasonal semen production in male dingoes and dingo-hybrids from eastern Australia (17 pure-bred and three dingo-hybrids) was also reported (Catling 1979). Dingoes are currently considered the ancestor of, or a close relative of, domestic dogs (Freedman *et al.* 2014; Smith 2015; Jackson *et al.* 2017). Although related species or breeds are likely to share reproductive characteristics, differences in reproductive seasonality between dingoes and domestic dogs have already been reported in both sexes – dingoes breed once annually whereas domestic dogs breed twice annually given they have 6–12-month interoestrus intervals (Green and Catling 1977; Catling 1979; Jones and Stevens 1988; Catling *et al.* 1992; Concannon 2011).

These differences were considered as part of the basis for phylogenetic differentiation between dingoes and domestic dogs (reviewed by Purcell 2010).

The reproductive cycle of dingoes is similar to that of the New Guinea singing dog (*Canis hallstromi*). This most closely related species to dingoes also breeds only once a year, but if the female fails to breed at the first oestrus, she can return to a second complete oestrus 8–16 weeks later (Koler-Matznick *et al.* 2001). In contrast, female domestic dogs typically have two oestrus cycles per year (Johnston *et al.* 2001). Additionally, rates of ovulation (97–100%) and pregnancy (86–100%) in the domestic dog are high (England *et al.* 2009). Some authors believe that this prolificity in domestic dogs is due to the greater rate of multiocyte follicles (MOF) present in their ovaries (Payan-Carreira and Pires 2008), also known as polyoocytic or polyovular follicles (Telfer and Gosden 1987; Reynaud *et al.* 2012). These are a group of oocytes (2–17 oocytes) that remain together inside the same follicle (Tingen *et al.* 2009). Although present at all follicular stages, MOF are more predominant at the primordial stage in prepubertal females, and at the secondary stage in adults (Lunardon *et al.* 2015). Despite the close phylogenetic relationship between dingoes and domestic dogs, we could not find any study reporting the occurrence of MOF in dingoes or dingo-dog hybrids.

Dingo-dog hybrids are sometimes thought to lack reproductive seasonality, with females having more than one oestrus cycle per year and males producing greater amounts of sperm throughout the year (Catling 1979; Catling *et al.* 1992). Some studies support this view, suggesting that these hybrids are likely to have enhanced fertility, as reported for hybrids between wolves (*Canis lupus*), and the genetics of most hybrids are typically dominated by dingo genes (M. Gentle, unpubl. data), probably reflecting the relatively recent introgression of domestic dog genes (since 1788) into dingo populations (see Stephens *et al.* 2015) and a lower survivorship of domestic breeds in the wild. Therefore, we hypothesise that dingo-dog hybrid reproduction will also be more similar to that of dingoes than domestic dogs. We test this hypothesis by measuring seasonal patterns of reproduction in female dingo-hybrids through examining the gross morphology of the uterus and detailed histology of their gonads, monthly, from samples collected over a four-year period.

Methods

Seventy-four female dingo or dingo-hybrids were foot-trapped and killed around urban areas in south-east Queensland and extreme north-east New South Wales by professional trappers employed by regional governments and other organisations, from 2012 to 2015 (Fig. 1). This study was part of a larger project on the ecology of periurban wild dogs conducted by Biosecurity Queensland (Animal ethics approval no.: CA 2013/01/660) and the University of Queensland (Animal ethics approval no.: SVS/145/13). Whole animals were stored at -20°C following collection. Location, date and time of trapping were recorded for each individual dingo collected. Trapping dates were classified into their respective season: autumn (March to May), winter (June to August), spring (September to November) and summer (December to February).

Of the 74 females used in this study, 22 were randomly selected for microsatellite genetic analysis (Wilton 2001; Stephens *et al.* 2015) conducted by the Biosecurity Queensland laboratory. Allelic data pertaining to reference samples of known dingoes and domestic dogs were used to categorise our samples as either (1) domestic dogs, (2) dingo-dog hybrids of varying proportions of dingo genetics, or (3) dingoes, based on the Average 3Q score, as reported by Elledge *et al.* (2008).

At necropsy, the two canine teeth from the top jaw were removed. Radiography was conducted at the University of Queensland Veterinary Medical Centre of both canine teeth. Tooth and pulp cavity width at 15 mm from the root tip were measured. The mean of these measurements from both teeth was used to calculate the age (in months) using the formula described

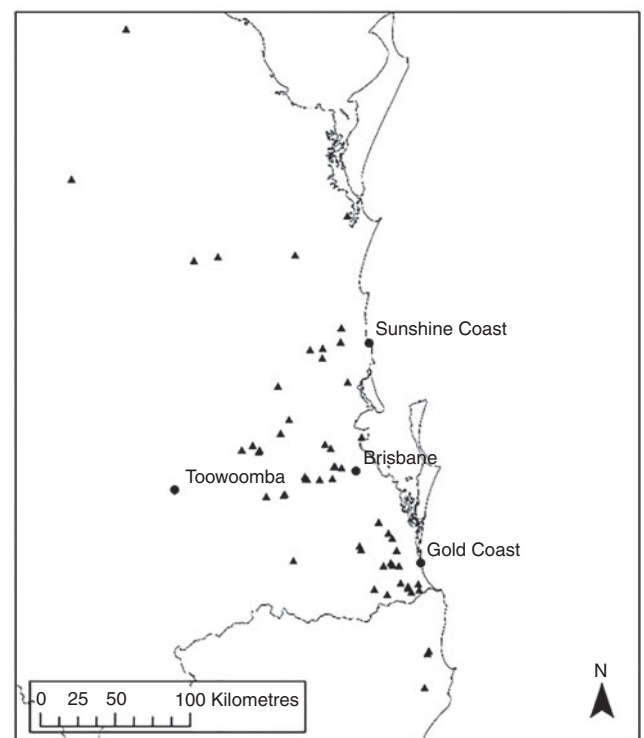


Fig. 1. Map of south-east Queensland showing the locations (triangles) where our sampled female animals were trapped from 2012 to 2015.

by Knowlton and Whittemore (2001). The study animals were therefore classified into the following age groups: pup (<6 months), young (6–12 months), young-adult (12–24 months), and adult (>24 months).

The reproductive tract was dissected from 71 females (of the 74) and stored for analysis at -20°C . Thawed uteri were weighed and the diameter from the middle and interswelling section of both horns was measured. Females with uterus diameters less than 4 mm were classified as primiparous and anoestrous females, between 4–7 mm as parous and anoestrous, proestrous or oestrous females, and more than 7 mm as pregnant or postpartum females (Jones and Stevens 1988). The presence or absence of uterine swelling was also recorded. After external analysis, the uterus was opened longitudinally to identify placental sites or 'scars' and the involution stages. Recent involution (1–3 weeks after parturition) was identified by the granular surface, with crenellated mucosa and presence of dark brown mucous and blood clots. The intermediary stage (4–7 weeks after parturition) was identified by light crenellated mucosa with a light brown mucous, and few or no haemorrhagic spots and blood clots. Older involution (8–9 weeks after parturition) was identified by a few spots with granulated mucosa, no mucous, and placental sites differentiating from the interplacental endometrium by being black/brown (Al-Bassam *et al.* 1981). Both ovaries were weighed and fixed in Bouin fixative for 12–18 h. For histology, the ovaries were divided transversally in two parts. The water within the tissue was replaced by a sequence of three ethanol dilutions (45%, 60% and 95%), followed by 100% xylene and filled with paraffin wax. These samples were then embedded with wax and were cut into sections using a microtome. The sections (3–5 μm) were placed and fixed on a microscope slide for further staining with haematoxylin and eosin. The slides were analysed on a light microscope by measuring the number of structures: Follicle I (diameter between 1–3 mm), Follicle II (diameter >3 mm), *corpus luteum* (CL), regressive *corpus luteum* (RG-CL), and multiocyte follicles (MOF). The size of follicles was measured using specific software for microscopy (Cell Sens Standard 1.12, Olympus Corporation). A Chi-square test was performed on the proportions of ages trapped in different seasons.

Results

Genetic analysis

Of the random sample of 22 females, 13.6% (3 of 22) were assigned as dingo, and 86.4% (19 of 22) as hybrids, and none were domestic dogs. Dingo genes dominated most of the females assigned as hybrid (>68%; 15 of 22), with only 18% (4 of 22) exhibiting less than 50% dingo genes (Table 1). The results confirmed that the sample represented dingo–dog hybrids. Similar proportions of hybrids have been reported in other studies (e.g. Stephens *et al.* 2015).

Female ages

In total, 74 females were trapped between 2012 and 2015. These comprised 18 pups, 26 young, 11 young-adults, and 19 adults. Significantly more pups ($\chi^2 = 8.22$, d.f. = 3, $P = 0.042$) were present in the trapped sample of females during the summer than other seasons.

Table 1. Genetic identity of 22 female wild dogs captured in south-east Queensland, 2012–15

Description	<i>n</i>	% of animals
Dingo	3	13.60
Hybrid (>75% dingo genes)	3	13.64
Hybrid (65–75% dingo genes)	6	27.27
Hybrid (50–65% dingo genes)	6	27.27
Hybrid (<50% dingo genes)	4	18.18
Domestic dog	0	0

Reproductive tracts

Uterine features

From the analysis of uterine diameter (number of females, mean \pm standard deviation), primiparous and anoestrous females were observed in spring (pup: $n = 5$, 2.66 ± 0.70 mm; young-adult: $n = 3$, 3.08 ± 1.84 mm) and summer (pup: $n = 8$, 3.51 ± 0.99 mm; young: $n = 7$, 3.91 ± 0.50 mm). Parous and anoestrous, or proestrous and oestrous females were observed in autumn (pup: $n = 1$, 5.9 mm; young: $n = 7$, 4.79 ± 1.97 mm; young-adult: $n = 1$, 4.35 mm; adult: $n = 3$, 6.55 ± 1.60 mm), winter (pup: $n = 2$, 4.47 ± 1.24 mm; young: $n = 8$, 5.25 ± 2.32 mm), spring (young: $n = 2$, 5.77 ± 0.25 mm; adult: $n = 2$, 5.80 ± 0.07 mm), and summer (young-adult: $n = 6$, 4.79 ± 0.82 mm; adult: $n = 9$, 4.82 ± 2.50 mm). Pregnant or postpartum females were observed only in winter (young-adult: $n = 1$, 8.25 mm; adult: $n = 5$, 12.55 ± 7.52 mm) (Fig. 2). Most uterine swelling and placental sites were detected from August to October, and mean uterine weight peaked in June (Fig. 3). The peak was particularly influenced by one adult female that had a uterine weight of just over 660 g. Seven of the other 16 females trapped in winter (3 young, 1 young-adult, and 3 adult) had uterine weights of 10–30 g. All pups ($n = 16$) and most young females (19 of 24) had uterine horns weighing less than 10 g. The few exceptions occurred in autumn ($n = 2$) and winter ($n = 3$), when the uterine horns weighed 10–20 g. Of the 71 animals, 15 presented placental sites. Recent placental sites were observed in four females, three in winter and one in summer. Intermediary involution of placental sites was observed in two females in spring and one female in winter. Old placental sites were observed mostly in summer ($n = 3$), in spring ($n = 2$) and in autumn ($n = 1$). The mean number of placental sites presented on uterine endometrium was 7.2 (± 2.04). Thus, the estimated mean litter size of animals in our sample of 71 females was 7.2 (± 2.04) pups per pregnancy.

Ovary features

CL and RG-CL were absent in pups. However, of the young females aged 6–12 months, eight (30.8%) had CL. Of these eight animals, two were sampled in autumn, four in winter, and two in spring. CL was also present in three of the 11 young-adult females. Of these three animals, one was trapped in winter and presented swelling in the uterine horns and placental sites, and two were trapped in summer. Of these two animals, one presented placental sites on the endometrium. Of the 19 female adults, six (31.6%) presented CL. Of these six animals, two were trapped in autumn, three in winter and one in summer. Of these two animals

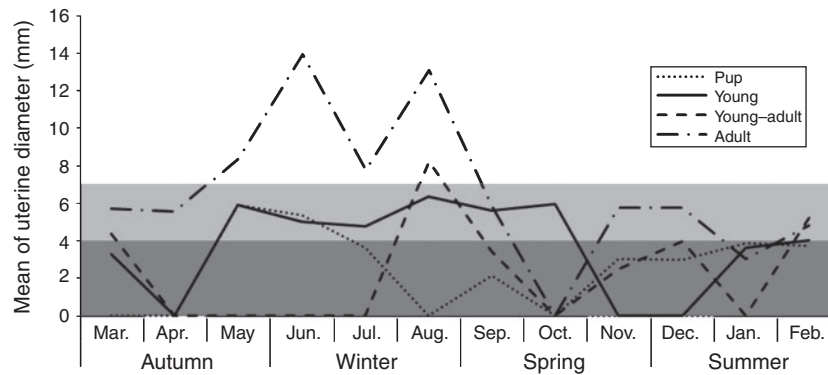


Fig. 2. Uterine diameter of dingo-hybrid during different seasons. Mean of uterine diameter of dingo-hybrid during different seasons (pooled from 2012 to 2015). The dark grey area in the graphic represents the primiparous uterus of anoestrous females with diameter <4 mm. The light grey area represents the parous uterus of anoestrous, proestrous or oestrous females with diameter of 4–7 mm. The white area in the graphic represents pregnant or postpartum uterus with diameter >7 mm.

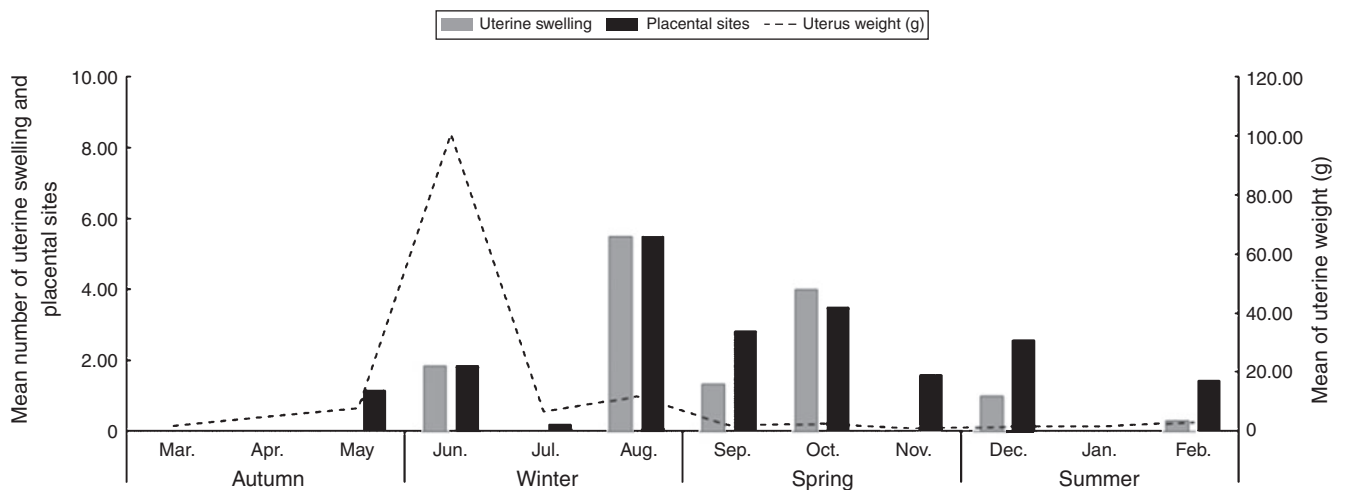


Fig. 3. Annual uterine features of dingo-hybrids. Mean number of uterine swelling, placental sites, and uterine weight, of female dingo-hybrids sampled monthly (pooled from 2012 to 2015).

with CL trapped in autumn, one presented placental sites. Of the three adult females with CL trapped in winter, two presented swelling and placental sites. The single adult female with CL trapped in summer showed uterine horn swelling and placental sites.

Ovary cycle

Growing follicles, 1–3 mm in diameter, were found in females of all ages. Most study animals (10 of 12, 83.3%) presented growing follicles in autumn, and few (3 of 13, 23.0%) had growing follicles during the spring. Potential follicles (3–5 mm) were rare and ovulatory follicles, greater than 5 mm, were not observed. As shown in Fig. 3, the follicular wave started in summer, increasing and reaching a peak in autumn and decreasing in winter, reaching the bottom in spring. The expected opposite trend was observed in CL with a peak in winter and a trough in spring and summer (Fig. 4).

Multiocyte follicles

No more than two oocytes were found inside the same follicle of any sample. MOFs were observed in 22.9% (16 of 70) of all females analysed. They were present mainly in early-stage follicles (Fig. 5a, b). Follicles at different stages were also seen sharing the same theca external, but separated by theca internal (Fig. 5c). Their prevalence was 22.2% (4 of 18) in adults, 18.2% (2 of 11) in young-adults, 20.0% (5 of 25) in young, and 31.3% (5 of 16) in pups. MOFs at primordial stage were not identified due to the difficulties of identifying agglomeration of primordial oocytes from MOFs.

Discussion

Our results indicate that dingo–dog hybrids exhibit breeding patterns more similar to those of dingoes than dogs, breeding once per year over the winter. The diameter and weight measurements

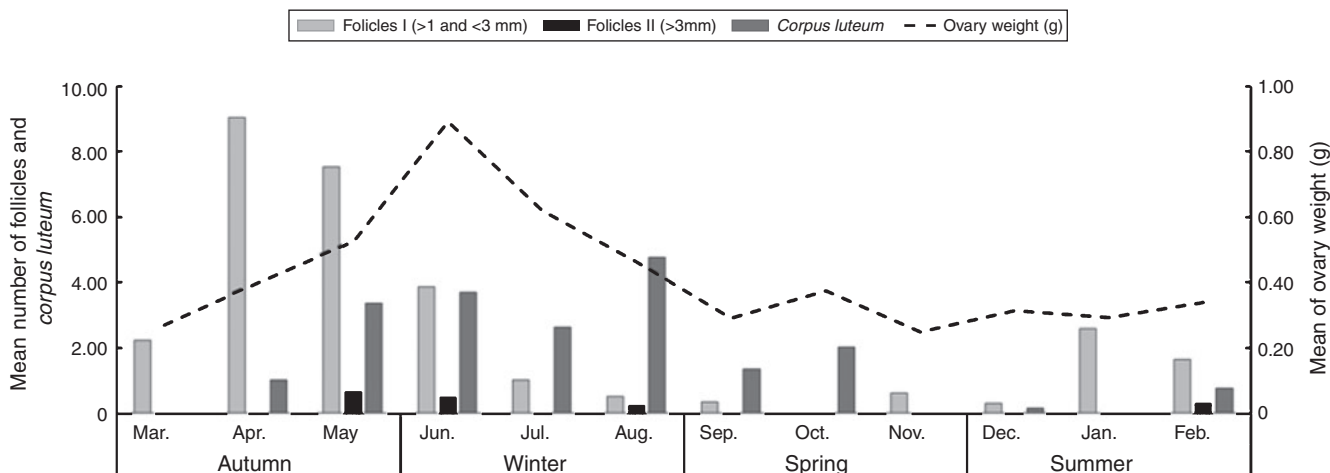


Fig. 4. Annual ovary cycle of dingo-hybrids. Mean numbers of follicles and *corpus luteum*, and mean ovary weight in female dingo-hybrids trapped monthly (pooled from 2012 to 2015).

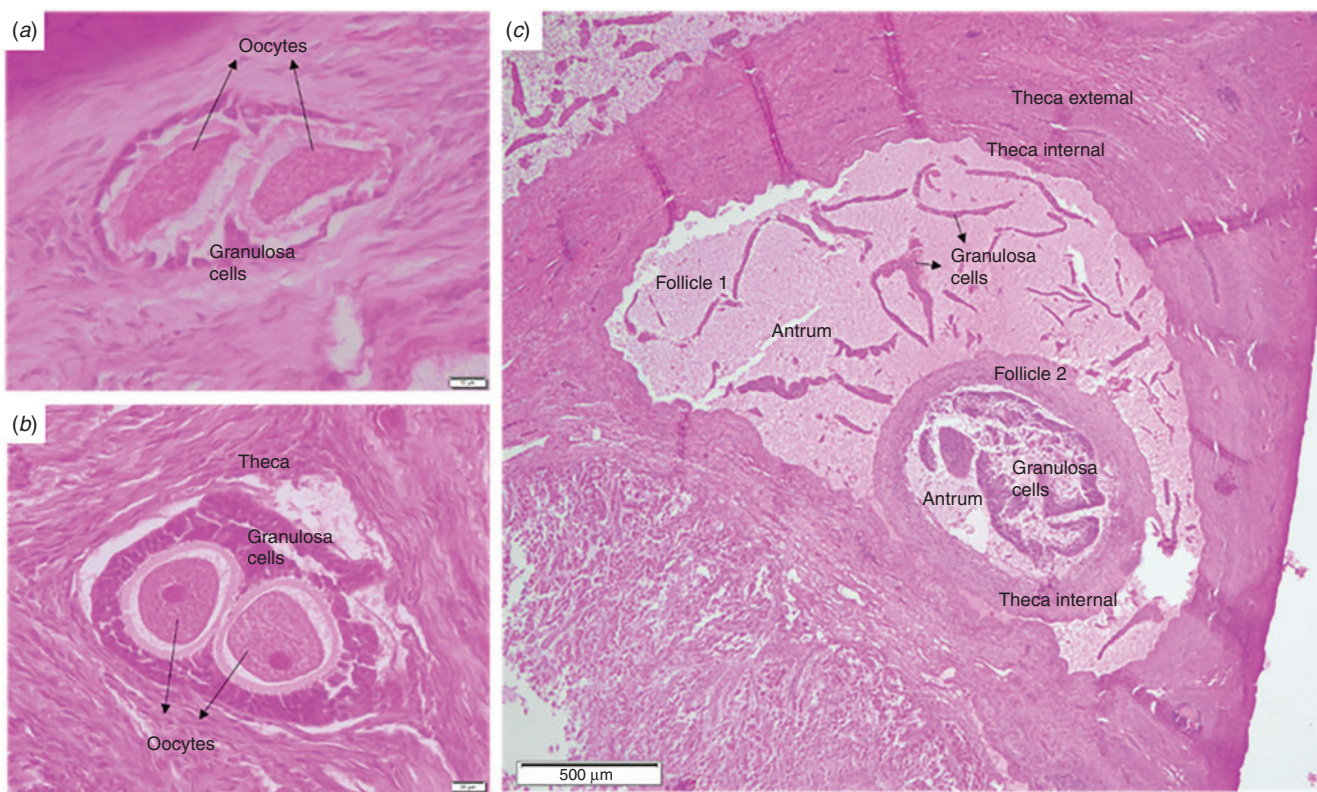


Fig. 5. Photomicrograph of a cross-section of multi-oocyte follicles in the ovary of dingo-hybrids, stained with haematoxylin and eosin. (a) Primary follicle with two oocytes sharing same granulosa cells layer (scale: 10 µm). (b) Secondary follicle with two oocytes sharing the same granulosa cells and theca layer (scale: 20 µm). (c) Two antral follicles (1 and 2) in different growing stages sharing the same theca external (scale: 500 µm).

of the uterus indicate that puberty can occur before 12 months of age in dingo-hybrids. Puberty in dingoes typically occurs between 12 and 24 months of age (Jones and Stevens 1988; Catling et al. 1992; Corbett 2001). The uterus analysis of pups (<6 months old) indicated primiparous and anoestrous females with an absence of CL in the ovary. Although most dingoes reach

sexual maturity in their second year or later, the presence of placental sites and observations of CL in the reproductive tract of younger dingo-hybrids clearly demonstrates that pubertal oestrus and pregnancy can occur before 12 months of age. These results confirm observations from field studies that show a small proportion of animals sometimes breed in their first year

(Allen *et al.* 2015). Early puberty in dingoes was described previously in younger females around 12 months old (Jones and Stevens 1988; Corbett 1988). Favourable environmental conditions (such as higher than average rainfall or resource subsidisation) can advance puberty in dingoes (Catling *et al.* 1992; Allen *et al.* 2015). However, from the three pure dingoes identified herein only two were less than 12 month old and none of them showed signs of early pubertal oestrus with uteri diameters less than 4 mm, and no follicles >3 mm were observed. Domestic dogs have their pubertal oestrus around 6–24 months of age; however, most of them reach their maximal reproductive potential only after the third or fourth oestrus (Johnston *et al.* 2001; Concannon 2011). We have two plausible, non-mutually exclusive explanations for these observations. First, the periurban and urban environment provides dingo-hybrids with favourable conditions for breeding (Allen *et al.* 2013b). Second, dingo-hybrids have inherited early pubertal oestrus from domestic dogs. Additional samples of pure dingoes are needed to investigate the possibility of inherited early pubertal oestrus in dingo-hybrids.

The higher proportion of pups obtained in spring and summer further support dingo-like breeding seasonality in hybrids, as described for dingoes in temperate and arid Australia (Jones and Stevens 1988). Winter (May to August) is known to be a predominant period of births in Australia (Corbett 2001). However, in northern Australia fewer births (4–8%) occur from November to February, and in south-eastern Australia low levels of births (1–6%) occur throughout the year (Corbett 2001). Dingoes are whelped and reared in spring and summer.

The pattern of changes in uterine weight we observed was consistent with the findings of Catling *et al.* (1992), revealing a pronounced peak in June. Recent placental sites were also mostly observed during winter. Depending on the swelling width and the intensity of haemorrhage at the spot, those placental sites are morphologically similar to those of domestic dog females that have whelped 1–4 weeks before (Al-Bassam *et al.* 1981), indicating that pups from those females were born in winter. The last involution stage (older placental sites) was mostly observed in females sampled during summer. The morphology of these placental sites without uterine swelling is similar to that reported for domestic dogs more than eight weeks after parturition (Al-Bassam *et al.* 1981), indicating that these study animals whelped at the end of winter or during the spring. It is possible that the uterine horn of dingoes takes longer to complete the endometrium involution, given that they have a longer period of anoestrus than domestic dogs. Unfortunately, there is no published information about uterine involution of post-parturient female dingoes to assess this possibility.

We found that the ovary follicular phase appeared to start in January. The number of follicles peaked in April and decreased over June and July, coinciding with when CL start to increase in number. Potential ovulatory follicles were observed in low frequencies in May and June, and also in August and February. It is important to note that although the potential ovulatory follicles were likely to ovulate, they were not ovulatory follicles, thus it is not possible to link their presence with ovulation. In female domestic dogs, the follicular phase involves a cohort of 2–8 detectable follicles (3 mm diameter) 6–10 days before the luteinising hormone surge (Concannon 2011). A detailed study in domestic dogs has reported growing follicles starting to

increase in number from Day –60 of ovulation, reaching a peak on Day –5, and large follicles (>4 mm diameter) can be identified from Day –10 to –1 of ovulation (England *et al.* 2009). In dingoes, follicles and CL larger than 3 mm occur only during the time of ovulation and postovulation (Jones and Stevens 1988). It is most likely that female dingo-hybrids in south-eastern Queensland ovulate from May to July, when a peak of growing follicles start to diminish and CL to appear. In addition, in both May and June, potential ovulatory follicles were observed with a subsequent increase in number of CL over May, reaching a peak in August. The peak of ovary weight observed in June was most likely caused by the presence of both CL and ovulatory follicles. The same pattern of ovary weight found in our study was also observed by Jones and Stevens (1988), in the Eastern Highlands of Victoria.

Potential ovulatory follicles found in females trapped in August and February were rare, with only one female recorded in these months. Given such isolated cases, it is not possible to attribute these to a second peak of ovulation. Female New Guinea singing dogs have one annual breeding season; however, they can have late pregnancies – females are able to have up to three subsequent oestrous cycles, 8–16 weeks later, if the female is not previously impregnated (Koler-Matznick *et al.* 2001, 2007). Live hybrid pups <2 weeks old were found during our study in mid October of 2014 (B. Allen, unpubl. data). This concurs with our combined observations of uterine weight, follicle development and CL peaks defining the once-annual reproductive period in female dingo-hybrids over winter. It is therefore likely that these isolated observations later than these times represent subsequent oestrous cycles (as in the New Guinea singing dog) rather than the absence of clear breeding seasonality (as per domestic dogs). Subsequent oestrous cycles have been reported previously in pure female dingoes (Smith 2015), but not in female dingo-hybrids.

The observation of MOFs more commonly found in younger than older dingo-hybrids is consistent with what Silva-Santos and Seneda (2011) found for younger domestic dogs. MOFs have been reported in the coyote (*Canis latrans*) (Kennelly *et al.* 1977), domestic dog (Telfer and Gosden 1987; Payan-Carreira and Pires 2008), rabbit (*Oryctolagus cuniculus*) (Al-Mufti *et al.* 1988), pig (*Sus scrofa domestica*) (Stankiewicz *et al.* 2009), mouse (*Mus musculus*) lines selected for high fecundity (Alm *et al.* 2010), goat (*Capra aegagrus hircus*) (Lucci *et al.* 1999) and cattle (*Bos taurus* and *Bos indicus*) (Silva-Santos *et al.* 2011). A difference in the frequency of MOFs between pure-bred dogs (25.5%) and mongrels (52.3%) has been attributed to increased fertility caused by hybrid vigour (Payan-Carreira and Pires 2008). The presence of MOFs does not increase fertility by ovulating all oocytes present inside MOFs, but by selecting the best oocyte (good quality and fertilisable) to finalise the development and ovulate (Reynaud *et al.* 2009, 2012). The presence of MOFs may likewise lead to the prolificacy of dingo-hybrids.

Our estimated mean litter size (7.2 ± 2.04) is greater than other averages reported previously (4–6 pups), all of which had similar sample sizes and used similar prenatal assessment methods (Jones and Stevens 1988; Catling *et al.* 1992; Corbett 2001; Allen *et al.* 2015). These are well conducted studies from across a variety of climate zones, and likely accurately represent

litter sizes in these zones and hence most of Australia. But the key point of difference between our sample and those of previous studies is that ours is derived from animals with a greater proportion and longer history of hybridisation. While hybridisation does not appear to influence breeding seasonality (as described earlier), it does appear to increase prenatal litter sizes, as found here and also by Catling *et al.* (1992). Prenatal litter sizes are possibly equal to the number of pups actually whelped by a female, but it is not known if this translates into any meaningful increases of population growth for free-roaming or wild populations. Hybrids' litter sizes might be larger, but environmental factors may still constrain actual population growth to levels similar to those experienced by dingoes. Additional studies on survivability of pups and early mortality factors are needed to investigate these issues.

Conclusion

Our data clearly show that female dingo–dog hybrids are more similar to dingoes than to domestic dogs with respect to breeding seasonality, with a once-annual breeding cycle. Hybridisation might convey some reproductive advantages to dingo–dog hybrids through the occurrence of multiocyte follicles (i.e. better quality and more-fertilisable oocytes) and increased litter sizes. However, we do not know (though it is probably unlikely) whether this translates into greater population growth. In conclusion, we recommend that future studies seek to understand the mechanisms and causes driving the breeding seasonality of dingo–dog hybrids. This knowledge may be useful for developing improved strategies for both the conservation and management of dingoes and dingo-hybrids alike.

Conflicts of interest

The authors declare no conflicts of interest.

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