Dingo visitation and behaviour at long-term scent-marking sites varies by sex and season

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Author contributions

BA designed the study, conducted fieldwork, completed data analysis, and wrote and edited the manuscript. BP and NJ contributed to designing the study, conducting fieldwork, and writing and editing the manuscript.

Declarations- data availability and conflicts of interest

The authors declare no conflicts of interest. All code and data used in this study are available online at github: https://github.com/Brendan-Alting

Keywords

Reproductive competition, mate-guarding, canid, territoriality, carnivore, camera-trap

Significance statement

Animals may use certain signals to reduce the risk of coming into direct conflict with other individuals. Many carnivores use scent marks to achieve this, and the role of scent marking in enforcing boundaries between territorial carnivores is well established. Conspecifics can avoid conflict (or notice opportunity) through the information these signals provide. Here we show that dingoes, a territorial Canid species, show varying patterns of scent marking throughout the year. Scent marking increased considerably during the three-month breeding season, and males scent marked more than females. Males also often marked over the top of a female’s scent mark. This indicates that for this species scent marking is not solely focussed on territorial defence, but that it also plays a role in monopolising mating opportunities.

Abstract

Many carnivores scent mark to communicate with conspecifics, and understanding seasonal and social patterns of scent marking can help to elucidate its function(s). Dingoes are mainland Australia’s apex terrestrial predator, with family groups (‘packs’) defending territories from neighbours and other conspecifics. In contrast to other wild canids such as wolves, coyotes, and African wild dogs, where patterns of scent marking are relatively well studied, little is known about scent marking in wild dingoes. Using camera traps at 10 dingo marking sites within the ranges of multiple dingo packs, we characterised seasonal visitation patterns and detailed scent-marking behaviour. Dingoes visited marking sites more frequently during the annual breeding season (March to May), at which time scent marking rates also increased. When an opposite sex pair visited a marking site together, males scent marked at higher rates than females, and were responsible for most first (60%) and last (73%) scent marks deposited during a visit. Tandem marking – sequential marking by both members of the pair - occurred at 97% of pair visits, and males were significantly more likely to overmark female scent marks than females were to overmark males. Taken together, these results suggest that scent marking plays a role beyond territorial advertisement in dingoes, and supports the hypothesis that male dingoes employ scent marking to mate guard females by advertising their presence/residence to other males, particularly during the annual breeding season.

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Introduction

Mammalian scent marking is the deposition of an odour by an animal through distinct behaviours such as urination, defecation, and rubbing, which occurs in specific locations or at landmarks (Kleiman 1966). Scent marking is ubiquitous amongst mammals, and has been observed in every carnivore species (Macdonald 1980). The roles of scent marking are varied and have been discussed and tested extensively in the literature, with communication between individuals and groups a major unifying theme (Buesching and Jordan 2019). The ubiquity of scent marking highlights its importance in carnivore sociality, and understanding behaviours associated with it can shed light on the evolution of carnivore social behaviour. Beyond the spatial distribution of scent marking sites which have been a key focus of olfactory communication studies in the wild (Gosling and Roberts 2001), elucidating the functions of mammal behaviour and movement also requires a focus on scent marking patterns temporally, and at an individual level (Buesching and Jordan 2019).

Animals may scent mark to advertise territory ownership (Claase et al. 2024), or in reproductive competition, either by advertising their health and availability to potential mates (Poirier et al. 2021), or in mate guarding (Lledo-Ferrer et al. 2010). Scent marking is an efficient form of territorial advertisement, as resident individuals or groups can avoid direct confrontations with competitors (neighbours or interlopers/intruders) that could otherwise result in injury or death to either party (Gosling 1982). Indeed, scent marking may be the primary way that individuals in adjacent territories interact, as direct encounters in some territorial species can be rare (e.g. African wild dogs, *Lycaon pictus*, Jordan et al. 2017).

Territorial scent marking strategies vary by species and environmental conditions, and may result in distinct spatial and temporal patterns. While some species, such as Ethiopian wolves *(Canis simensis*), preferentially scent-mark along their territorial borders (Sillero-Zubiri and Macdonald 1998) others, such as marmosets (*Callithrix jacchus*), mark consistently throughout their territories (Lazaro-Perea et al. 1999). These spatial patterns of marking are often context dependent and vary with territory size and resources, even within the same species. For example, in spotted hyenas (*Crocuta crocuta*), when resources are plentiful, clans have smaller home ranges making a boundary scent marking strategy economically feasible (Kruuk 1972), while in areas where hyenas have larger home ranges, they scent mark throughout their territory instead, as boundary marking would be economically unviable (Gorman and Mills 1984). While the spatial distribution of scent marks has garnered much research attention, information on the spatial distribution of scents alone offers little more than an indication of the intended recipient (Buesching and Jordan 2019). Rather than acting as a ‘keep-out’ signal, the scent-matching hypothesis posits that by linking scent marks deposited by a territory owner within a territory, an intruder recognises the potential costs of intruding on this territory (Gosling 1982). Given the resident’s past investments in marking and defending that territory – regardless of whether it is on the territory border or spread within it - the presence of their scent is an honest signal of their willingness to defend the territory (Gosling and Roberts 2001a).

While territorial advertisements are clearly important, in some mammalian species scent marking can increase around key breeding periods (Gese and Ruff 1997), suggesting a direct role in mate choice or mate defence, particularly in species that hold territories year-round. Some scent marks can be honest signals of individual health (e.g. house mice (*Mus musculus)*, Zala et al. 2004) and status (e.g. tamarins *(Saguinus spp.),* Poirier et al. 2021), potentially allowing animals to evaluate the quality of potential mates prior to breeding (Hurst and Beynon 2004). Further, different chemical signals in female scent marks may serve to signal sexual receptivity (Coombes et al. 2018). For species with distinct annual breeding periods, including all Canid species bar domesticated dogs *(Canis lupus familiaris)*, this information can be invaluable, as opportunities to breed are seasonally limited (Macdonald et al. 2019). This helps to explain why scent marking behaviour may increase in reproductive periods, and suggests that scent marking serves multiple purposes that are likely not limited to territorial – or at least spatial - defence in many species.

Numerous explanations have been posited regarding the role of scent marking, and its fine-scale attributes may shed further light on its function(s). Species often exhibit sex-specific behavioural differences at scent marking sites (Claase et al. 2024). In territorial species with high reproductive skew and in which dominant pairs monopolise, or attempt to monopolise, breeding (Bell et al. 2014), the importance and prevalence of tandem marking, in which two opposite sex individuals both scent mark, has been well established, such as in meerkats (*Suricata suricatta*) (Jordan 2007) and coyotes *(Canis latrans)* (Gese and Ruff 1997). In some species, such as African wild dogs, scent marks deposited by an individual are often ‘overmarked’ by another, usually a male, with that individual leaving a scent mark on top of the previous individual’s scent (Jordan et al. 2014). Overmarking between mated pairs has been studied extensively in rodents, and in some cases may serve to mask the scent of the other paired individual (e.g. golden hamsters, *Mesocricetus auratus*, Johnston et al. 1994). This behaviour has been observed in coyotes, and may represent a form of mate guarding, in which one individual, usually the male, marks over the other member of the dominant pair, purportedly to conceal the mark of the other (Gese and Ruff 1997). The order of scent placement, too, has been shown to be important, with scents deposited most recently given more attention in a number of mammal species (Johnston et al. 1997; Fisher et al. 2003). Finally, overmarking may combine the scents of the individual members of a dominant pair, advertising to adjacent packs and intruders the presence of a breeding pair in a territory (Jordan et al. 2016), although this theory has less empirical support (Ferkin and Pierce 2007).

Canids (species in the family *Canidae*) are territorial and consistently mark within their territories (Allen et al. 1999). Canids broadly share similar reproductive strategies, with a dominant pair in a pack reproducing once in a year, and the remainder of the pack composed of offspring from previous years and some pups (Lord et al. 2013). As a purportedly monogamous group (although extra-pair paternity is increasingly being identified among many species, such as Arctic foxes (*Vulpes lagopus*) (Cameron et al. 2011), African wild dogs (Spiering et al. 2010) and Ethiopian wolves (*Canis simensis* (Randall et al. 2007)), both the dominant male and female contribute to territorial defence. For males, initial energy investment in offspring production is low relative to the costs borne by females, but consequentially males can never be completely sure of the paternity of offspring (Baker et al. 2004). For dominant males that rear dependent young that are not their own, this is a significant fitness loss (Macdonald et al. 2019). While females may defend their territory for exclusive resource access to raise young, male territorial defence, and scent marking within their territory, could potentially be an attempt to stop competing males from breeding with their paired female.

Dingoes (variously referred to as *Canis dingo*, *Canis familiaris*, *Canis lupus dingo*, amongst others), are a nominally socially monogamous canid present across most of mainland Australia (Thomson et al. 1992; Allen and West 2013). Dingoes are similar to other canids in their breeding behaviours, with territorial packs consisting of a dominant breeding pair, their offspring from previous years, and recent pups (Thomson 1992). Extrapair paternity has also been noted in dingoes (Tatler et al. 2021). Dingoes breed once a year, and females are sexually responsive in oestrus for approximately 2 weeks, anywhere between March and May (Catling et al. 1992, Thomson 1992). Dingo scent marking has previously been studied in the context of how scent marking behaviours are affected by lethal control on a population (Wallach et al. 2009), as well as the investigation of dingo scent marks by foxes (Wooster et al. 2021), and other mesopredators (Banks et al. 2016). Dingoes frequently scent mark their territory (Thomson 1992) and respond to the scents of conspecifics (Walker et al. 2024) and thus are a good model species for exploring the functions of canid scent marking behaviour.

Here we use camera trap videos positioned at known scent marking sites used by a population of wild dingoes that have been under study since 2019 (Alting et al. 2024), to describe visitation patterns and detailed scent marking behaviour throughout the annual cycle, and potentially discern some of the roles of scent marking for a socially monogamous canid. Dingoes hold territories year-round (Thomson et al. 1992), and due to their generalist behaviour and a temperate climate in this region, food is available throughout the year. Seasonal anthropogenic food resource pulses associated with holiday periods are present, particularly in summer (Alting et al. 2024), and natural resource pulses such as washed-up seabirds on the beach can provide resources (ABC 2023), although these are infrequent and unreliable. If dingo scent-marking was exclusively related to territorial defence related to resource availability, we would expect year-round visitation with no seasonal peaks, and consistent scent-marking behaviour patterns throughout the year. If, however, dingoes scent mark more in the breeding and pre-breeding period than in other times of the year, then we may infer that scent marking plays a role in reproductive availability and competition for mates. Dingoes would still be expected to scent mark throughout the year if scent marks serve to advertise territories to adjacent packs (Allen et al. 1999), although potentially at lower rates outside the breeding season. Finally, we may expect different scent marking responses of males and females during the breeding season. Females may increase scent marking during the breeding season to advertise to potential mates (including intruding males and unrelated males within their pack). Male dingoes may be expected to overmark their female breeding partner to conceal the female’s scent mark (Johnston et al. 1994), or indicate a willingness to defend access to the female (Gosling and Roberts 2001b). Together, these patterns would suggest that mate guarding of females is occurring for this species, as it does in some other canid species.

Methods

*Study site and dingo population*

This study was conducted in coastal New South Wales, Australia, on Worimi country in the Great Lakes region (centred on 32.492° S, 152.343° E). This area is used for multiple purposes, and consists of urban areas, private land, National Park (Myall Lakes), and Mid Coast Council managed land. Scent marking sites identified in the area all occurred on national parks estate, which is composed of woodland, coastal heath, dunes, and small patches of littoral rainforest (NSW STVM 2023). Dingoes occur throughout the study area, and pack locations and demographics for individuals born in the area have been collected since 2019. Dingo pack dynamics and resident individual animals are known and documented (Alting et al. 2024), and dingo packs in the area occupy essentially non overlapping home ranges. Targeted lethal baiting of dingoes does not occur in our study site, but dingoes are lethally controlled (trapped and shot) if an individual exhibits aggressive behaviours towards humans.

*Marking site identification*

Marking sites were monitored from 2020-2023, and were initially identified using a domestic dog trained to identify dingo scent marks. The dog was taken to suspected scent marking areas, particularly at junctions of trails and roads. If the dog detected dingo scent, it would sit next to the location of the urine mark. Camera traps (Browning Strike Force HD pro) were placed on the opposite side of the trail or road, high in trees to avoid theft, and aimed at the junction, with the camera centred on the location the dog indicated had dingo scent. Initial visits by dingoes were reviewed and the positioning of cameras adjusted/refined to better centre on the areas used by the dingoes during visits. In some locations where the marking site could not be covered by a single camera’s field of view, two camera traps were placed at the site. This process occurred across Myall Lakes National Park, to obtain spatial variation in scent marking sites and to capture the behaviour from several different packs.

Cameras were set to record 30s videos, with no delay in trigger time, and high sensitivity. We aimed to service camera traps at least monthly, but covid-related lockdowns and flooding events prevented this. Consequently, cameras were serviced a mean average of every 43 days (range = 7-295). We placed cameras at 22 possible sites in total, from which 10 marking sites were identified and monitored throughout the study (mean distance between sites = 4083m (range = 1498-8072). Any videos that captured humans were discarded.

*Video data extraction*

Behaviours were recorded from videos by one researcher (BA) for any dingoes detected at the sites. We recorded the number of individuals in each video sequence, and classified individuals by sex and age category (adult or juvenile (<1 year old)). Dingoes could usually be identified to the individual level, using a dingo identification database from the area documenting unique natural variation in sock and pelage patterns described previously (Alting et al. 2024), and this allowed accurate classification of age category, sex, and pack membership. Dominants were defined as pairs seen consistently together, observed mating, or bearing pups (Gese and Ruff 1997; Mech 1999). Adult male and female dingoes very rarely associate with one another unless they are either a dominant pair, or subdominant related siblings in their natal pack (Tatler et al. 2021). Related siblings could be removed as their pack status was known as they were seen as juveniles throughout the study. Where possible, unknown individuals were sexed based on the presence of visible teats (females) or the presence of a visible penile sheath (males). Age categorisation of unknown individuals was based on size. If we were unsure of any of these, we left the value as ‘unsure.’

For specific behaviours, we recorded the specific ‘deposition point’ identity (a unique identifier) within each scent marking site at which scent marks occurred, the substrate on which each deposition point was initially placed (tree, shrub, ground, grass), the duration (seconds) of each behaviour, and whether the dingo sniffed the ground or not when at the site (sniffs required a minimum 3 seconds of nose to ground). Scent marking behaviours included sniffing a specific deposition point (Fig 1c) (separate to ground sniffing; nose within 5cm of deposition point and pointed down), urinating on a deposition point (either squat (Fig 1a) or raised leg (Fig 1d), defecating, and raking (Fig 1b) (repeatedly scraping the ground with its fore or hind feet). If dingoes came to a site, but did not sniff or scent mark, we recorded this as a ‘no response’ behaviour. We also recorded the duration that each individual was present in the marking site, with the start and end of the duration defined as the entry or exit of the dingo from the field of view of the cameras. Camera traps sometimes triggered after the onset of a behaviour, or stopped filming during a particular behaviour. In these instances, we transcribed the part of the event was seen, and recorded whether we missed the start, end, or both start and end of the site visit. We used events where we missed a part of the visit for temporal analysis of dingo seasonal visitations to scent marking sites, but restricted analysis of fine scale scent marking behaviours to sequences where we could identify all behaviours that occurred between the dingo or dingoes entering and exiting the site.



*Figure 1: Two dingoes displaying various scent marking behaviours in the Myall Lakes region of Australia. a) A female dingo performing a squat urination; b) the same female raking the ground; c) A male dingo sniffing the scent mark placed by the female in a & b; d) the same male performing a raised leg urination over the scent mark placed by the female in a & b.*

*Data analysis (seasonal patterns)*

All marking sites were not continuously monitored throughout the year, due to camera battery failure and theft. To account for missing survey effort in seasonal analysis, we assigned each day of the year as camera ‘active’ or ‘inactive.’ We then restricted data to overall independent visits (visits by any adult dingo >30 minutes apart) to scent marking sites, and counted detections per active camera trap night. We then summed data for each month of the year. Across the ten camera stations used, we obtained data from at least 2 years for every month of the year (mean active trap nights = 571.1, range = 367-889). To identify different factors associated with seasonal trends, we ran three generalised additive models (GAMs) in the *mgcv* package, which are appropriate for time series data (Wood 2017). First, we categorised each event as either including a lone adult dingo, or including dingoes in an adult pair consisting of one male and one female. We also calculated the mean duration spent at the site, for each individual dingo per visit to each site, and divided this value by ten to ensure variables were on the same scale. For GAM (a), we included the sum of visits per month as a response variable, and included total visits (lone + paired visits), only paired visits, and time spent at site, as predictor variables, and included ‘year’ and ‘site ID’ as random effects. For GAM (b), we used sum of visits per month as a response variable, and included whether a dingo ‘sniffed’ (investigated) during a visit, as a predictor variable, with ‘year’ and ‘site ID’ as random effects. Finally, for GAM (c), we used the sum of events per month as a response variable, and included counts of ‘urinations’, ‘defecations’, and ‘rakes’ as predictor variables, with ‘year’ and ‘site ID’ as random terms. For each model, we included ‘month’ with a cyclic cubic regression spline, with k=4, approximating distinct seasons in dingo behavioural ecology, and a negative-binomial distribution, suitable for over-dispersed count data (Gardner et al. 1995). To account for camera effort, for each model we summed the number of cameras that were active for each day and each month in total, and used this as an offset (log). We evaluated significance of model terms by evaluating associated p-values and estimated degrees of freedom (edf), where a higher ‘edf’ implies more curvature in the model term, and defined a significant result as one where p<0.05.

Data analysis (fine-scale behaviour)

Where a dominant pair visited a site together, we recorded and analysed their fine-scale marking behaviours. To analyse the likelihood of a dingo overmarking a scent at a deposition point, we calculated whether dominant dingoes marked at a deposition point, dependent on whether the opposite sex had marked before, and how many scent marks had previously been deposited at the deposition point during that visit. We ran ‘glmms’ with a binomial distribution in the R package *lme4*, with ‘over mark’ as a binary response variable (y/n), and the predictor variables ‘number of marks previously left at site’, with an interaction variable of ‘sex of marker’ and ‘sex of most recent scent mark’, for each event (Bates et al. 2015).We also included a random effect of ‘site ID’ to account for repeated measures at that marking site. We evaluated the importance of predictor variables by calculating effect sizes with 95% confidence intervals (Halsey 2019).

Finally, to examine likelihoods of each sex leaving a mark in a given order where marking occurred on a given deposition point at a site, we extracted the ‘first’ and ‘last’ marks deposited there during each visit; recording whether they were placed by the male or female. To look for sex-specific patterns in either first or last markers on a deposition point, we used a binomial test of proportions without a continuity correction to test if these were significantly different to an even chance (50/50 marks at each by a male or a female). We also extracted the number of marks placed on each deposition point during a visit, with the sex of the depositor of each marker also recorded. For each mark in sequence, we used a binomial test of proportions without a continuity correction to test whether one sex was more likely to deposit at that point in the sequence (model d).

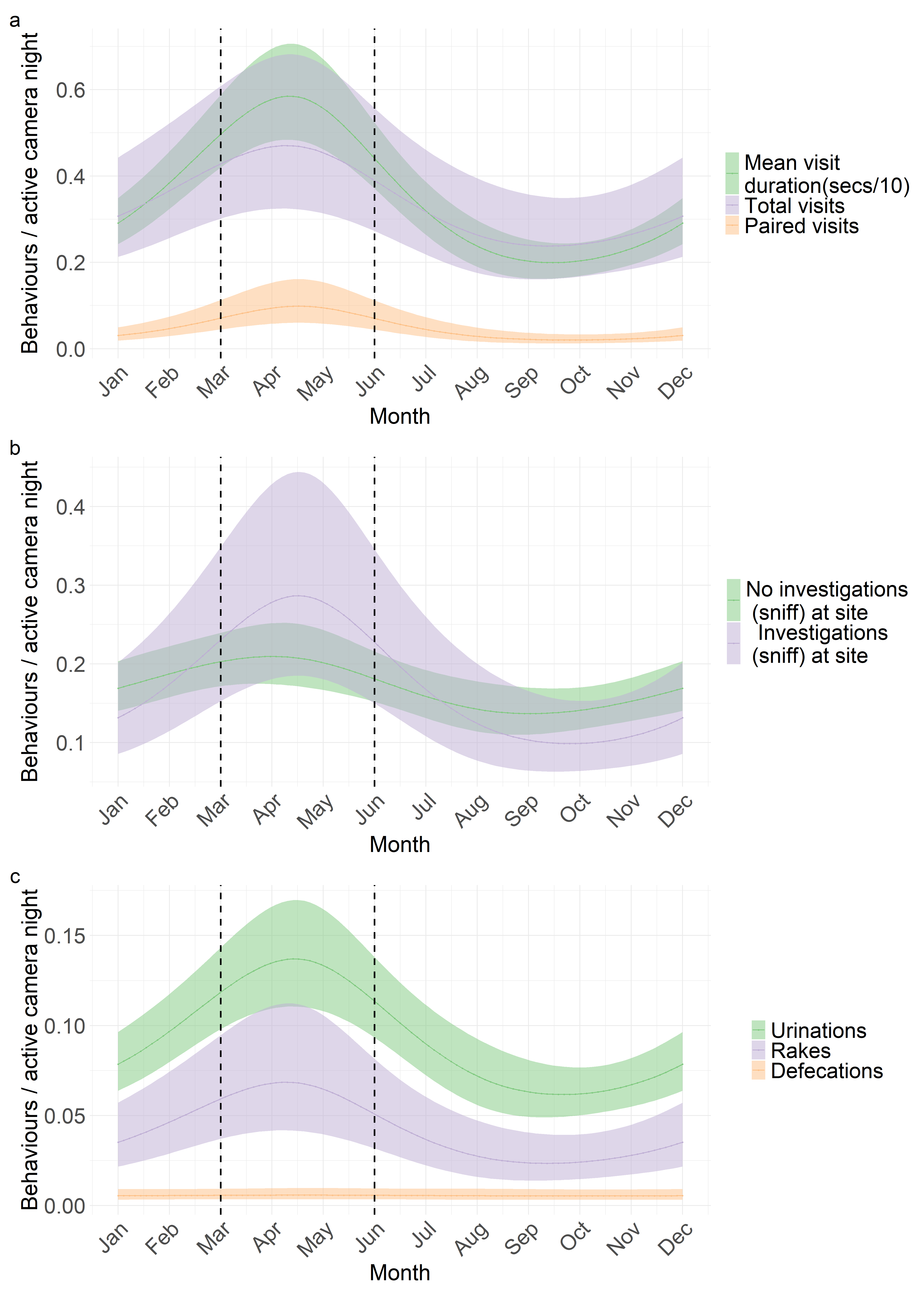
All work was conducted under scientific licence SL102716 and approval 22/102A from the UNSW Animal Ethics Committee. It was not possible to record data blind because our study involved focal animals in the field.

Results

We observed 2375 independent visits by dingoes across the ten marking sites, with a mean of 237.5 events from all cameras (sd=217, range= 46-685 events), and 5479 individual behaviours in total. An average of 1.44 (sd=0.81, range = 1-7) dingoes (including adults and juveniles) were present during each visit to a marking site. In total, we observed 1045 adult male visits, with 539 male urinations (rate = 0.52 urinations/ visit), and 783 adult female visits, with 281 female urinations (rate = 0.36 urinations/ visit). We recorded 1923 ‘no-response at site’, 2275 sniffs, 383 rakes and 56 defecations. We recorded 367 events where both a male and female dominant dingo were present at a site simultaneously, and where at least one of the pair investigated a deposition point.

*Seasonal results*

The random effect site ID and year were significant for all GAMs (supplementary materials). Total visits (edf = 1.743, p<0.001), paired visits (edf = 1.896, p <0.001) and time spent at site (edf= 1.880, p <0.001) all varied by month (Fig 1a). Total visits and paired visits to sites peaked in April. Length of time spent at site was longest in April and shortest in September. Both investigating at a site (edf = 1.843, p <0.001) and ‘no responses’ when visiting a site (edf = 1.421, p =0.03), differed depending on month (Fig 1b). Investigations and ‘no-responses’ when at site both peaked in late April/ early May. Urinations (edf = 1.744, p <0.001) and rakes (edf = 1.795, p <0.001) varied depending on month, peaking in April, whilst we found no evidence defecations varied with month (edf = 0.228, p = 0.330) (Fig 1c).



*Fig 2: Generalised Additive Model predicted results with 95% confidence intervals, evaluating the relative occurrence of different dingo behaviours at scent marking sites, from the mid-coast of NSW, Australia* ***4.2a****: Visit duration at marking sites, total visits to marking sites, and paired visits to marking sites.* ***4.2b****: Visits to sites with investigations (where dingo walked through site and sniffed deposition site), and visits to sites without sniffing.* ***4.2c:*** *Behaviours exhibited when at marking sites. Figures made in ggplot2 (Wickham et al 2024).*

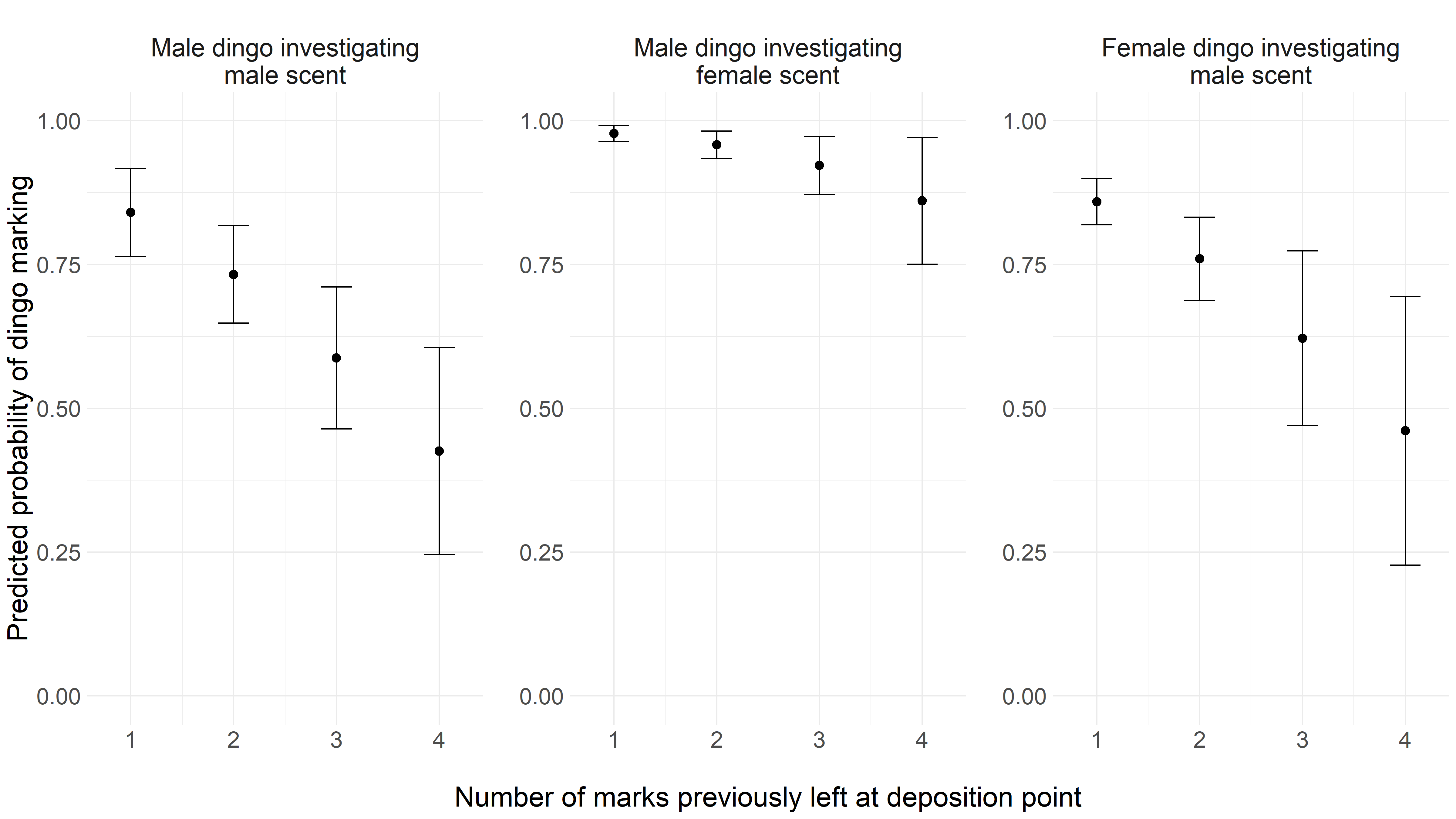
*Overall trends in fine-scale marking*

Male dingoes, if sniffing a scent mark placed by females, marked over it 100% of the time when that female’s scent mark was the first at the site (53/53 events), while females marked over males 85% of the time when that scent was the first at the site (55/65 events). Males overmarked females 90% of the time when that scent mark was the second at the site (28/31 events), and 100% when it was third (1/1 events) and fourth (2/2 events). If males sniffed their own scent, they marked over it 72% of the time in total (21/29 events). Females sniffed their own scent marks only twice in the entire study, and did not overmark them either of these times.

For both sexes, rates of overmarking declined with the amount of scent marks previously left at the site. Females rarely investigated sites if more than one scent mark had already been placed at a site (58 investigates of 1st male scent mark, 10 investigates in total of 2nd, 3rd and 4th scent marks). Males investigated female scent marks regardless of whether they were first or second (47 investigates of 1st female scent mark, 31 investigates of 2nd scent mark), but this declined for 3rd and 4th scent marks, as females rarely left these marks.

*Overmarking models*

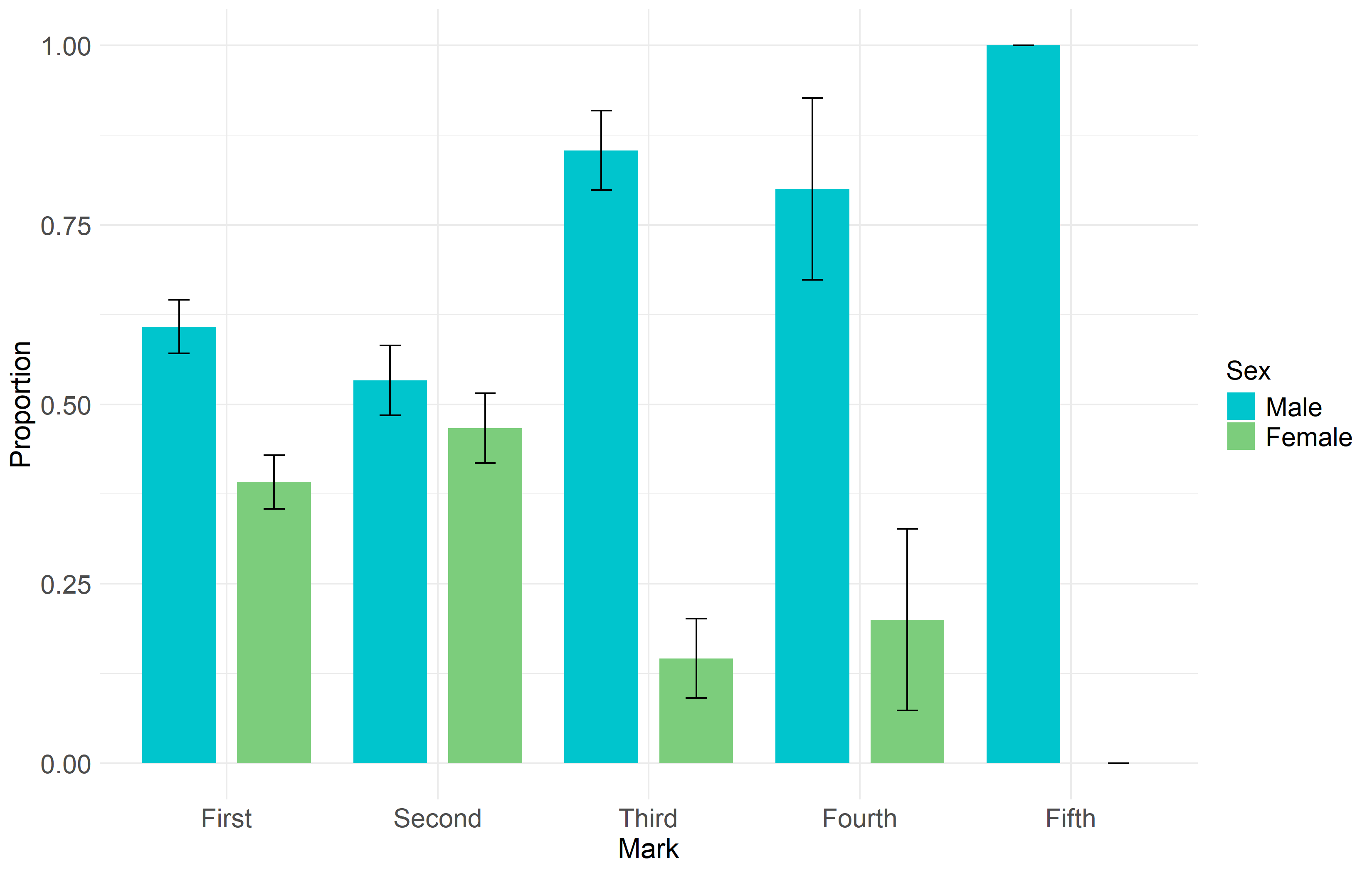
Only two events were recorded where females investigated female scents (both did not overmark), and so these events were excluded from the model. Site ID had no influence on the likelihood of an individual overmarking. There was a negative effect of the number of scent marks previously deposited at a deposition point (during the same visit) and the likelihood of a dingo overmarking when investigating (est = -0.654, 95% CI = -1.29 - -0.018). Whether a male was investigating a male scent had no influence on whether the male overmarked (est = -0.144, 95% CI = -1.331-1.044), compared to females investigating male scents (Fig 2). Males were more likely to overmark female previous marks (est = 1.975, 95% CI = 0.610-3.339) than females were to overmark males (Fig 3).



*Fig 3: GLMM predicted estimates of the likelihood of an individual dingo overmarking a scent mark after investigating it. Females investigated female scents only twice during the study, overmarked them neither time, and were removed from modelling.*

*Marking order modelling*

During visits by pairs, male dingoes were significantly more likely to mark first (binomial test of proportions, probability of mark= 0.608, 95% CI = 0.535-0.678, p<0.001) and last (binomial test of proportions, probability of mark = 0.727, 95% CI = 0.657-0.790, p <0.001) at a given deposition point (Fig 4). When previous markers were not accounted for, “middle marks” (those leaving neither the first nor last marks on a deposition point), were more evenly shared between the pair, suggesting that males were actively choosing to mark first and last. Male and females marked second at a site in proportion to expected given random chance (binomial test of proportions, probability of mark = 0.530, 95% CI = 0.435-0.623, p =0.579) (Fig 4). Males were more likely to mark third (binomial test of proportions, probability of mark = 0.854, 95% CI = 0.708-0.944, p <0.001), but not fourth (binomial test of proportions, probability of mark = 0.8, 95% CI = 0.444-0.975, p =0.109) or fifth (probability of mark = 1, 95% CI = 0.158-1, p = 0.5). This was likely due to small sample size (only 10 fourth and 2 fifth marks in total).



*Figure 4: Proportions of scent marks placed by male and female dingoes, depending on the order of the scent mark placed at each deposition point, when visited by a pair of dingoes (one female and one male).*

Discussion

*Overall results*

In common with other species, we found sex and seasonal variations in dingo scent-marking site use. Overall, males marked more often than females, including initiating more scent marking bouts and disproportionally leaving the final scent mark during each site visit. When males sniffed a female’s scent mark, they nearly always overmarked it with their own, while females only overmarked approximately 80% of male marks they sniffed, with this proportion declining with the number of scent marks already left at the site. Visitations to scent marking sites increased markedly in the breeding season, but visits were shorter than visits outside the breeding season. Together our results suggest that scent marking in dingoes plays a key role in dingo breeding behaviour, and in particular male mate advertisement or mate guarding of females.

*Seasonal trends*

While spatial patterns of marking dominate the scent marking literature, temporal patterns of marking have been investigated in many species, with many increasing visits in the breeding season (Olson et al. 2008), or establishing and using marking sites around that time (Nie et al. 2012). In species holding year-round territories, as most canid species do (Johnson et al. 2002), annual fluctuations in marking site visitation can indicate their function. Dingoes increased their visits to scent marking sites during the pre-breeding and breeding period compared to other times, with both total and paired (dominant male and female) visits increasing during this period (Fig 2a). This aligned with existing literature from other canid species (e.g. African wild dogs, Claase et al. 2022) and our expectation for dingoes, and suggests that scent marking plays an important role in dingo breeding behaviour, as it does for other species such as wolves (Llaneza et al. 2014; Thiel and DeWitt 2022) and coyotes (Gese and Ruff 1997; Schell et al. 2016). It is possible that elevated visitation to scent marking sites in the breeding period simply reflects general increases in dingo movement during this time. This is particularly relevant to the denning period at which time some canid species, such as African wild dogs, switch to a central place foraging strategy in which home range size shrinks (Pomilia et al. 2015). However, temporal changes in different behaviours such as sniffs and urinations at sites suggest an active motivation to visit and communicate via these sites.

Scent marking can be achieved using an array of excretory or glandular products, each potentially providing different information to receivers (Ralls 1971; Ferkin 2019). For example, while scats may provide some information on diet (Gorman 1990), the chemical compositions of urine may indicate oestrus (Gocinski et al. 2018), or parasite load (Mitchell et al. 2017). The temporal distribution of different forms of dingo scent marks showed contrasting patterns throughout the year, potentially reflecting the motivation of dingoes to convey different information at different times. Urination events at marking sites increased considerably during the breeding season, perhaps facilitating female advertisement of sexual availability (Coombes et al. 2018) as occurs in binturong/bearcats *(Arctictis binturong)* (Green et al. 2016). Urinations can provide an honest signal of mate quality (Gosling and Roberts 2001), with healthier individuals able to produce more attractive marks (Zala et al. 2004). For species with distinct periods of sexual availability, as in dingoes (Cursino et al. 2017), advertising sexual quality and availability through scent marks would be most important immediately prior to and during the breeding season.

Raking behaviours in dingoes increased in March and April, aligning with other studies that show increases in raking by canids in the breeding season (Sillero-Zubiri and Macdonald 1998). Canids have eccrine glands in their footpads (Meyer and Tsukise 1995), which can transmit olfactory information and are recognised by conspecifics (McClanahan and Rosell 2020). Raking the ground may be a way of depositing scents at a site, while also producing a visual signal to conspecifics, which may function to advertise to observers at the time of ground raking, and for encounters after the fact (Bekoff 1979). However, little is known of dingo ground raking and its function, and further studies are needed. Further, rates of defecations did not vary seasonally in our study area. Whilst it has been suggested that scat deposition may play a role in dingo social behaviour (Wallach et al. 2009), our findings agree with a study that found a lack of predictability in scat deposition by dingoes (Allen 2012), perhaps implying that scats do not play a major role in dingo communication during the breeding season.

Sex biases in scent marking during the breeding season have been noted in many species (Nie et al. 2012), and in pair-bonded territorial mammals it is usually males that mark more than females, e.g. in meerkats (Jordan 2007) and coyotes (Wells and Bekoff 1981). Male mate guarding of females has been proposed as a cause of this increase in scent marking, at least for territorial pair-bonded species. For example, male African wild dogs and coyotes overmark their paired female scent marks, possibly to conceal the mark of the dominant female from other males (Gese and Ruff 1997; Jordan et al. 2014). We observed more adult male dingo events at scent marking sites, and higher rates of urinations when at these sites (0.52 urinations/ visit for males vs 0.36 urinations/ visit for females). It seems likely that this is related to mate-guarding behaviour of females by resident males. Males may have an incentive to follow females as closely as possible, to ensure that they do not breed with other males, a behaviour commonly known as mate-guarding (Alberts et al. 1996). Such behaviour can involve physical guarding of the female (Setchell et al. 2005), and/or signalling of the presence of a mated pair in the territory through overmarking (Dunbar and Buehler 1980). Indeed, we detected an increase in paired visits to marking sites in May, which is approximately when female dingoes are likely to be sexually receptive (Cursino et al. 2017), supporting the idea of male mate guarding of females for this species.

*Fine-scale behaviours*

Scent marks can be expensive to produce (Gosling and Roberts 2001), and this implies that individuals will not mark more than they need to convey their intended message. Therefore, were scent marking solely related to advertising sexual availability to their respective partner, we would not expect males to mark twice at a site, for example if they had been overmarked by a female, as she would have gained the information from one mark. However, we found that males overmarked females at a very high rate, often marking several times at a site. This suggests an alternate role for scent marking apart from advertising reproductive availability to a partner, likely one in which male resident dingoes may be attempting to conceal the scent of female scent marks from rival conspecifics, as occurs in other canids (Jordan et al. 2014), or strongly associate their own scent with it.

How receivers perceive multiple scent-marks on a given deposition point (i.e. over-marks) depends on placement order (Ferkin and Pierce 2007). Some laboratory rodents, for example, respond most strongly to the most recent scent in a deposition point (Johnston et al. 1994), and in wild settings too, dominant individuals in many species such as some primates (Heymann 2006), leave the ‘top’ mark at a site more often than subordinates do, suggesting a communication benefit to doing so. We found that male dingoes left the final mark at a deposition point significantly more than females, and that males left the first mark at the deposition point more than females did, when a pair visited a site. This adds further weight to the argument for male mate guarding of females driving dingo marking behaviour. Whilst processing marking site videos, we observed numerous occasions of males marking at a site, appearing to wait for females to overmark them, before subsequently overmarking the female. On one occasion, after scent marking on a tree, a male dingo left the site, but returned to the site (some 60m) after apparently hearing the dominant female raking after overmarking, to overmark again (Supp video 1). Males often illustrated clear vigilance behaviour when at scent marking sites, and while females overmarked and watched males on the first scent occasion, they often left the site after marking once. In this context, it appears that females are content with advertising their presence at marking sites with one scent mark, while males are focussed on advertising ‘ownership’ or the presence of a pair, by repeatedly overmarking the female scent to ensure their mark is on top.

*Conclusions*

That scent marking plays at least some role in reproductive behaviours for dingoes seems clear. Scent marking as a behavioural process has been studied little in dingoes. Thomson et al (1992), reported that urinations of male dingoes increased in the breeding season, while Allen (2012), found that scat deposition of dingoes varied randomly throughout the year. Both of these findings agree with our study results. Much of mammal communication is achieved through scent marks (Ralls 1971), and every species that is known to hold territories also scent mark (Gosling 1982), highlighting its importance in territory maintenance. Indeed, for dingoes scent marking was a year-round process, and was not strictly related to breeding, despite increasing during breeding periods. While in some parts of the year, for example in the denning season, scent marking may function to protect food resources for a resident group (Bekoff and Wells 1982), in the breeding season scent marking may switch to functioning to defend mates from other rival individuals, particularly for males.

Territorial carnivores can pose numerous problems for land managers, and understanding how their behaviours change seasonally is key to managing their impacts (Valeix et al. 2012). Contextualising different scent marking strategies in the context of breeding seasons can help explain variations in movement and behaviour at different times of the year, and may even permit the use of anthropogenically manipulated scent marks (artificial or natural) to alter dingo movements (Robley et al. 2015), as in African wild dogs (Hansen et al. 2024). While our study suggests that dingo scent marking behaviour is similar to that found in other canids, with males marking more than females, and scent marking increasing during the breeding season, further studies are required to understand how other factors, such as the spatial distribution of scent marks across a territory, can convey information to conspecifics.

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