

**NOTE**

# Escort service: Sex and relatedness of humpback whales accompanying mother-calf pairs off Western Australia

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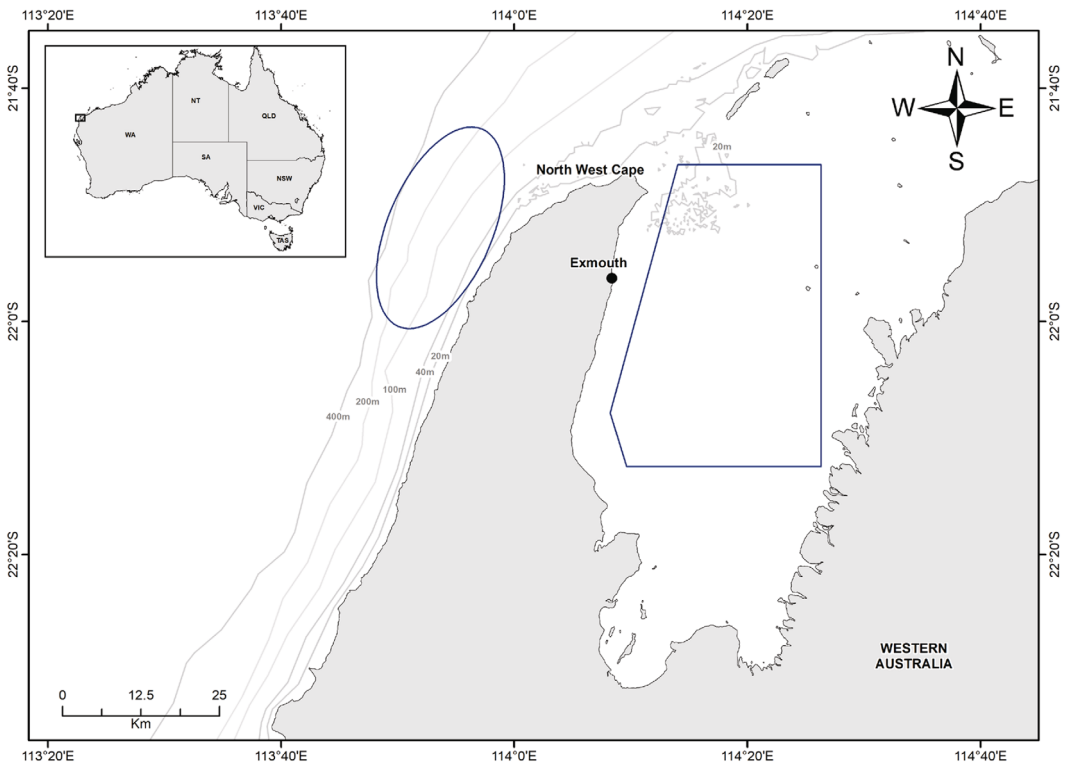
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The evolution and maintenance of group living in animal societies can be attributed to the benefits that individuals gain by being part of a group (e.g., increased resource acquisition and predator avoidance, Marcoux, 2008; enhanced opportunities for mating, Hamilton, 1964), but these can also include challenges (e.g., increased disease transmission, enhanced detection by predators, food and/or mate competition, Hughes, 1998). Factors that may influence the choice of associations include age, sex, reproductive condition, social status, and kinship (Alexander, 1974).

Groups consisting of closely related individuals form the basis of the social structure in many mammal species, including some whales and dolphins, e.g., killer whales (*Orcinus orca*), Pilot et al. (2010); bottlenose dolphins (*Tursiops* spp.), Möller et al. (2006); sperm whales (*Physeter macrocephalus*), Gero et al. (2009). However, cooperative behaviors can also evolve in the absence of kinship via alternative and/or complementary mechanisms, including reciprocity, manipulation, and mutualism, or may represent costly displays (reviewed in Clutton-Brock, 2009).

Among baleen whales, humpback whales (*Megaptera novaeangliae*) are found in all oceans and most populations undergo annual migrations from high latitude feeding grounds to low latitude breeding grounds (e.g., Calambokidis et al., 2000; Dawbin, 1966; Rasmussen et al., 2007). Their social structure is sometimes described as solitary (Mann & Karniski, 2017), but small fission-fusion pods (Weinrich et al., 2006) to large super groups (Findlay et al., 2017) are also observed. The species' mating system has been described as moderate polygyny, with a skew in the operational sex ratio and a degree of male competition for mates (Cerchio et al., 2005).

One of the largest populations of humpback whales is the Breeding Stock D (BSD) population of Western Australia (WA), with estimates of 20,000–30,000 individuals (Salgado Kent et al., 2012). These humpback whales migrate along the coast of WA, from Antarctic feeding grounds to warmer waters where they breed in the austral summer (June to November; Gales et al., 2011). During these months, humpback whales occur at Ningaloo Reef and in Exmouth Gulf (hereafter Ningaloo) in WA (Figure 1), which is an important calving area (Irvine et al., 2017).



**FIGURE 1** Map of the study area in Western Australia, showing the main study sites along Ningaloo Reef (West) and in Exmouth Gulf (East) (within blue shapes).

During their first year of life, humpback whale calves remain with their mothers for feeding, protection, and development (Acevedo-Gutierrez, 2009; Clapham, 2000). Mothers bear one offspring at a time, which is weaned before the birth of the next (Clapham, 1996), with past calving intervals of 2–3 years (Barendse et al., 2013). Mother-calf associations are believed to increase the offspring's reproductive success due to the learning of essential skills (Lindström, 1999), making it a pivotal time in a humpback whale's life cycle. Humpback mother-calf pairs are sometimes accompanied by male escorts (Herman & Antinaja, 1977) on their breeding grounds and along migratory routes. Adult escorts swimming near mother-calf pairs are generally thought to be males searching for mating opportunities (e.g., Herman et al., 2011; Mingramm et al., 2020; Spitz et al., 2002; Tyack, 2009), and on occasion males will challenge an escort for accompanying the pair (Spitz et al., 2002). However, other escort behaviors have raised questions about mechanisms driving their association with mother-calf pairs.

One such behavior is when escorts interfere with killer whales that are attacking humpback whale calves. Killer whales are the main predators of humpback whales, and they prey mainly on calves (Pitman et al., 2015, 2017). Over the past 20 years, reports of killer whale attacks on humpback whales have increased, suggesting that they may be becoming more common in some populations around the world (e.g., Capella et al., 2018; Naessig & Lanyon, 2004; Pitman et al., 2015, 2017; Saulitis et al., 2015).

At Ningaloo, at least dozens of humpback whale calves are predated upon by killer whales each year (Pitman et al., 2015), with observations in recent years suggesting numbers could be much higher (Toterdell pers. obs.). In this area, humpback whale calves were estimated to be killed in 67% of attacks during one calving season (Pitman et al., 2015). During these predatory events, humpback mothers attempted to protect their calves by trumpeting, guiding them to shallower waters, or lifting them out of the water using their head or back (Pitman et al., 2015).

When escorts were present during the attacks, they were observed to position themselves between the killer whales and the calf, trumpeting, charging at the attackers, and fin or fluke slapping, but on some occasions, they moved away and provided no apparent help (Pitman et al., 2015). The reason for this variation in escort behavior, and what the benefit to escorts for interfering in a killer whale attack would be, is still unclear (Pitman et al., 2017).

Proposed explanations for the role of escorts in humpback whales include kin selection (Pitman et al., 2017), altruism (whereby the escort receives no benefits), and pre- and/or postcopulation mate guarding (Clapham, 1996; Mobley & Herman, 1985), or “bodyguard” hypothesis (Cartwright & Sullivan, 2009; Mesnick, 1997), although the latter remains speculative (see Craig et al., 2014). The kin selection hypothesis for escort behavior could have evolved if an escort is closely related to the mother and/or the calf, and gains fitness benefits through cooperating with the pair. Humpback whales tend to migrate along similar routes annually, and there is evidence of maternally directed fidelity to breeding grounds (Baker et al., 1990), suggesting that related individuals may be able to interact with each other. It is therefore possible that escorts may be genetically related to the mother-calf pairs they accompany. Pairs of escorts that associate with a mother-calf pair could also be potentially related to each other and be cooperating to achieve access to females, although there is little evidence so far of close associations between genetically related adult humpback whales (e.g., Cypriano-Souza et al. 2010; Pomilla & Rosenbaum, 2006; Valsecchi et al., 2002; Weinrich et al., 2006). The aim of the current study was to determine if genetic relatedness (and sex of the escort) plays a role in humpback whale escort behavior at Ningaloo. We did this by genetically sexing the escorts and determining whether they were closely related to the mother and/or calf that they accompanied. We confirmed that all sampled escorts were males and that escorts were unrelated to the mothers and calves that they accompanied. Genetic relatedness and kin selection were thus rejected as potential explanations for humpback whale escort behaviors, and further explanations for these should be explored.

Ningaloo Reef is a fringing coral reef system on the west coast of North West Cape, Western Australia (WA, Figure 1). Humpback whales on the western side of the Peninsula are predominantly observed traveling through the area during their northern and southern migrations (Pitman et al., 2015). Biopsy samples of skin and blubber were collected from free-ranging humpback whales ( $n = 158$ ) in the area from July to October between 2013 and 2017. We used a Barnett crossbow and darts with a tip that extracted biopsy samples  $25 \times 4$  mm in size. Biopsy sampling was conducted opportunistically on both east (Exmouth Gulf) and west (Ningaloo Reef) sides of North West Cape (Figure 1).

Samples were mainly collected from whale pods consisting of an escort, mother, and calf. Mother-calf pairs (MC) were observed for approximately 10 min to determine if an escort (or escorts) was present. Groups from which not all individuals were sampled, as well as lone adults, were included to contribute to the analyses and population genetic (allele frequency) data. In total, 34 escorts, 44 mothers, 21 calves, and 59 additional adults were sampled (Table S1). Samples were stored in vials with 95% ethanol and later frozen.

DNA was extracted from skin samples using the salting-out method (Sunnucks & Hales, 1996), and bead cleaned if required (details in supplementary material). After that, 107 of 158 samples were considered of good quality for sequencing (Table S1). Individuals were sexed by amplifying fragments of the *ZFX* and *SRY* genes following Gilson et al. (1998), with thermocycler profile as in Möller & Beheregaray (2001) (additional information in supplementary material). All individuals, except one escort ( $n = 157$ ), were successfully sexed.

To develop the SNP data set, double-digest restriction-site associated DNA (ddRAD) libraries were prepared following the protocol of Peterson et al. (2012), with modifications as in Brauer et al. (2016) and Sandoval-Castillo et al. (2018). A subset of 96 high-quality samples was selected for library preparation to be sequenced in one Illumina lane. Priority was given to samples that were part of a pod containing an escort, i.e., MCE pods. Details about sequencing and single nucleotide polymorphism filtering are given in the supplementary material. The raw SNP catalog consisted of 157,097 SNPs (Table S2). Filtering with stringent criteria resulted in 10,002 unlinked SNPs being retained (Table S2), creating the final, high-quality data set to be used for relatedness analyses.

COANCESTRY v1.0.1.9 (Wang, 2011) was used to conduct the relatedness analyses. COANCESTRY enables calculation of pairwise relatedness between individuals using seven relatedness estimators. It also allows users to determine the

best performing estimator for their data set, including its accuracy and precision, through simulations using allele frequencies from empirical data (details in supplementary material). The triadic and dyadic maximum likelihood estimators had the most consistently narrow range in each kinship category for both simulations (Figure S1). They also had the highest correlation coefficients (99.89%) to the true value in both simulations, with and without missing data and genotyping error (Tables S4 and S5). As there was no difference between the two likelihood estimators, the triadic maximum-likelihood estimator, which was previously used in other cetacean studies (e.g., Zanardo et al., 2018), was chosen for this data set and used for further analyses.

The empirical relatedness estimates from all individuals were compared to the simulated values for the different kinship categories to identify dyads in the population exhibiting these relationships. Pairs sampled in the same pod (Table S3) were then examined for their degree of relatedness to determine whether they fitted within the ranges of simulated kinship categories. Mean relatedness was calculated for each type of escort association within a pod, i.e., mother-escort (ME), calf-escort (CE), and escort-escort (EE). Significant differences in the average relatedness within and between whale pods were tested using 1,000 permutations in *COANCESTRY*. Relatedness of ME, CE, and EE pairs sampled in the same pods (within pods; Table S3) were compared to relatedness of escorts to other mothers, calves, and adult males, respectively, in the population (between pods). This was to determine whether escorts were associating at random, or preferentially with mothers, calves, or other males that were less, or more, related to themselves. This was tested across all sampling years by including all individuals, and by testing only those sampled in the same year that an escort and its pod were sampled (albeit small sample sizes within some of the years).

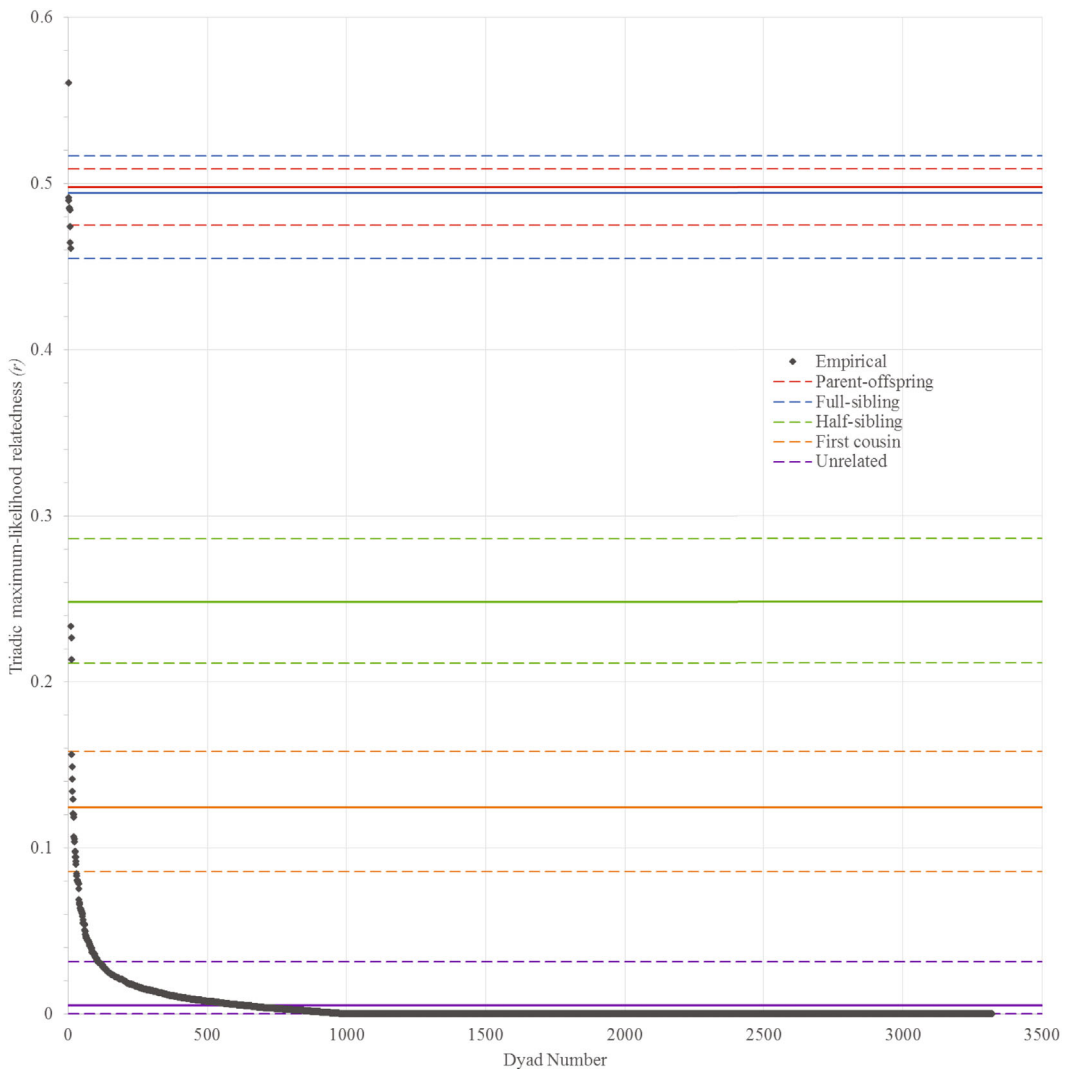
All sexed escorts ( $n = 33$ ) were males, suggesting that male whales generally perform the role of escort at Ningaloo, which is consistent with the sex of escorts along other migratory routes and breeding grounds (e.g., Cypriano-Souza et al., 2010; Félix & Botero-Acosta, 2011; Spitz et al., 2002). All individuals labeled as the mother ( $n = 44$ ) during field sampling were females. Among sampled calves, there were twice as many males sampled ( $n = 14$ ) than females ( $n = 7$ ).

Pairwise relatedness between all individuals revealed most dyads (98.04%) across the sampled population exhibited relatedness estimates within the ranges of simulated kinship categories (Figure 2). Most dyads were unrelated ( $n = 3,227$  dyads, 97.17%), with the next most frequent simulated kinship category observed being 3rd degree (e.g., first cousins;  $n = 18$  dyads, 0.54%; Figure 2). One dyad of nonassociated females sampled in 2016 showed the highest estimated relatedness ( $r = 0.56$ ), above both the averages calculated for parent-offspring and full-siblings, and three dyads had relatedness values expected for half-siblings and/or avuncular relationships ( $r \sim 0.25$ ; Figure 2).

As expected, all MC pairs sampled were highly related (range:  $r = 0.44$ – $0.49$ ), with estimates close to the theoretical value expected for parent-offspring relationships ( $r = 0.5$ ). Mean relatedness between ME from the same pod was very low ( $0.00057 \pm 0.00143$ ; Table 1). Similarly, relatedness between CE from the same pod was very low ( $0.00405 \pm 0.00816$ ; Table 1). Thus, no escort was closely related to either the mother or calf that it accompanied. Also, of the three EE that were sampled in a pod together, none of the pairs showed high relatedness values ( $M = 0.0027 \pm 0.0047$ ; Table S6). According to one of the simulations (with missing data and genotyping error), the relatedness for unrelated individuals is expected to be between  $0 \geq r \leq 0.03$ , which includes all EE relatedness estimates within pods (Table S6).

No significant differences were found in the average relatedness between ME pairs from the same pod (within pods) compared to escorts and mothers in the sampled population (between pods; Table 1). In addition, no significant differences were found in the average relatedness between CE within pods compared to between pods (Table 1). These results were also not significant when testing samples across all years, or in a single year (Table 1). Also, EE that accompanied a MC pair together (i.e. MCEE pod) were not more or less significantly related to one another compared to other adult males in the sampled population.

Humpback whale escorts are generally thought to be males interested in mating with the noncalf female they accompany (Clapham, 1996; Mobley & Herman, 1985), but why they assist mothers to protect calves from predation is still unclear. One such proposed mechanism is kin selection, where escorts may be protecting calves because they are closely related to the mother and/or calf, and are therefore gaining fitness benefits by doing so.



**FIGURE 2** Triadic maximum-likelihood relatedness between humpback whales (*Megaptera novaeangliae*) ( $n = 3,321$  dyads) sampled at Ningaloo, with the mean (solid line) and range (minimum and maximum; dashed line) of five kinship categories calculated through a simulation with 1% missing data and 3% genotyping error.

Here we found that kin selection is unlikely to be the mechanism driving escort associations and the protective behavior of calves in Ningaloo, as escorts were unrelated to both the mothers and calves whom they were associating with. We also found that escorts (all genetically confirmed to be males) did not preferentially associate with females that were less (or more) genetically related to them. In addition, when two escorts were observed accompanying a mother-calf pair at the same time, relatedness estimates indicated that the two males were unrelated to each other. Unrelated pairs of males in coalitions were also found in Brazilian (Cypriano-Souza et al., 2010) and (eastern and western) African humpback whales (Pomilla & Rosenbaum, 2006). Although the preponderance of two or more males escorting a female with or without a calf are found in competitive contexts (e.g., Baker & Herman, 1984; Tyack & Whitehead, 1983), there is some evidence that pairs of males may sometimes cooperate in attempts to secure a female (e.g., Clapham et al., 1992; Darling et al., 2006; Pack et al., 1998). The results of our study, in

**TABLE 1** Relatedness using the triadic maximum likelihood for humpback whale (*Megaptera novaeangliae*) dyads of different age and sex classes sampled within and between pods along Ningaloo Reef and in Exmouth Gulf, Western Australia ( $p > .05$  for all comparisons of within vs. between pods).

Sampling years	CE		ME		EE	
	WP	BP	WP	BP	WP	BP
2014	—	—	0 (4)	0.0034 (12)	—	—
2015	0.0065 (6)	0.0058 (18)	0.0009 (5)	0.0013 (35)	0.0041 (2)	0.0016 (56)
2016	0.0030 (6)	0.0043 (18)	0 (7)	0.0024 (105)	—	—
All Years <sup>a</sup>	0.0041 (14)	0.0044 (154)	0.0006 (17)	0.0025 (614)	0.0027 (3)	0.0029 (216)

Note. MC: mother-calf; ME: mother-escort; CE: calf-escort; EE: escort-escort; WP: within pods; BP: between pods. Mean relatedness (number of dyads).

<sup>a</sup>All years = 2014–2017; no pod data available for 2013. In 2017 only one ME pair sampled, so no year comparison presented. Blank sections of the table were where not enough individuals were available to calculate differences ( $n < 2$ ).

combination with those above support the idea that kin selection is unlikely to explain the male escort behavior observed in humpback whales.

Although not many studies have explored genetic relatedness in baleen whale groups, their longevity, wide dispersal, promiscuous breeding system and calving intervals do not appear to support the maintenance of close-kin relationships (Wiley et al., 2011). Our study agrees with findings based on humpback whales sampled at feeding grounds and migratory routes, which showed no associations between genetically related individuals, except for mother-calf pairs (Pomilla & Rosenbaum, 2006; Valsecchi et al., 2002; Weinrich et al., 2006). Thus, alternate hypotheses to kin selection need to be explored to understand why escorts associate with humpback whale mothers and assist them in protecting their calves from predation. Additional genomic, physiological, and behavioral studies of humpback whales at Ningaloo should help with answering these questions.

## AUTHOR CONTRIBUTIONS

**Lucy-Rose Seeary:** Formal analysis; investigation; writing – original draft; writing – review and editing. **Catherine R. M. Attard:** Formal analysis; investigation; supervision; writing – review and editing. **John Totterdell:** Conceptualization; funding acquisition; investigation; project administration; writing – review and editing. **Robert L. Pitman:** Conceptualization; investigation; writing – review and editing. **Luciana M. Möller:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; project administration; supervision; writing – original draft; writing – review and editing.

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