

Mate Guarding in Male Dall's Porpoises (*Phocoenoides dalli*)

Pamela M. Willis & Lawrence M. Dill

Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada

Correspondence

Pamela M. Willis, Ecology, Evolution and Behavior Program, Integrative Biology, 1 University Station C0900, University of Texas at Austin, Austin, TX 78712-0253, USA.
E-mail: pmwillis@mail.utexas.edu

Received: June 16, 2006

Initial acceptance: September 7, 2006

Final acceptance: January 8, 2007

(S. Forbes)

doi: 10.1111/j.1439-0310.2007.01347.x

Abstract

Mate guarding, whereby a male closely attends and defends a fertile female from extra-pair matings, is one mating tactic males of many species use to protect their paternity. Although female defense occurs in many species of terrestrial mammal, comparable examples among cetaceans are largely absent, potentially as a result of the wide dispersion and mobility of females and their prey. Here, we investigate whether the close association of individual male Dall's porpoises with individual females during the breeding season is consistent with mate guarding. As mate guarding is predicted to be costly, and in other taxa is often associated with a reduction in foraging efficiency, we also examine whether males trade-off this activity with time at depth. Males maintained longer associations and closer distances with female partners than with male ones. They also surfaced in greater synchrony with, and more often approached, their female partners than male ones. In contrast to males with male partners, males paired with females engaged in agonistic interactions with other adult males, and infrequently affiliated with extra-pair individuals. These data suggest males are actively attempting to maintain their associations with females, while also acting to reduce female extra-pair copulations and increase their own paternity. Guarding males also undertook shorter dives than non-guarding males, suggesting that they trade-off time at depth with guarding. Such a trade-off is likely to involve a reduction in foraging opportunities, due to a decrease in time spent at foraging depth. Mate guarding in this species may be facilitated by the relatively smaller size and decreased mobility of newly calved, estrous females, particularly if females also benefit from guarding.

Introduction

Opportunities for sperm competition arise whenever fertile females mate with multiple males. Males may attempt to minimize the risk of sperm competition, and increase their assurance of paternity, by increasing sperm delivery to females and/or preventing potential rivals from copulating (Birkhead & Möller 1998). Mate guarding, where a male closely attends a female over her fertile period to deter rival copulation attempts, is a common paternity guard in a variety of taxa (e.g. Birkhead 1979; Cothran 2004;

Pelletier 2005; Saeki et al. 2005; Setchell & Wickings 2006).

Among cetaceans, males generally appear to rove in search of receptive females, spending little time with them other than to mate (reviewed in Connor et al. 2000a; Schaeff, in press). In contrast to terrestrial mammals, neither resource defense, nor the defense of multiple females, is known to occur among cetaceans, and the defense of individual females appears to be uncommon. The wide dispersal and high mobility of female cetaceans and their prey may limit opportunities for, or relative benefits of,

mate guarding (Connor et al. 2000a; Schaeff, in press). However, in a few taxa, males escort or form consortships with individual females during the breeding season (Tyack & Whitehead 1983; Wells et al. 1987; Connor et al. 1992). Such males appear to be increasing their sexual access to females, and defending or deterring them from extra-pair matings (Clapham 1996; Connor et al. 2000a,b; Watson 2005). Interestingly, male bottlenose dolphins primarily do so in alliance with other males (Connor et al. 1996; Moors 1997), perhaps because defending individually is ineffective or unprofitable (Connor et al. 1996).

Male Dall's porpoises also form associations with individual females during the breeding season, as we describe below. Although the close association of a male with a fertile female is often interpreted as mate guarding, it may serve a variety of functions, such as increasing sexual access (e.g. through courtship displays or coercion), deterring predation, or strengthening the pair bond (reviewed in Gowaty & Plissner 1987; Birkhead & Möller 1992). The mate guarding hypothesis predicts the close attendance of individual females during fertile periods, along with the exclusive prediction that males will attempt to reduce female encounters with other males. Here we investigate whether male Dall's porpoises behave towards females and males in ways consistent with mate guarding.

Mate guarding necessitates monitoring female movements, maintaining proximity, and monitoring and challenging potential rivals. In addition to being energetically costly, these behaviors compete temporally with other activities important to survival and/or reproduction (Alberts et al. 1996; Sparkes et al. 1996; Low 2005; Saeki et al. 2005). Males trade-off mate guarding with behaviors such as foraging (Westneat 1994; Alberts et al. 1996), pursuit of alternate mating opportunities (Chuang-Dobbs et al. 2001), and predator avoidance (Cothran 2004). As attending to females may require changes in male diving behavior, we investigated whether male Dall's porpoises trade-off mate guarding with time spent at depth, thereby reducing opportunities for foraging.

Methods

Study Population

We studied Dall's porpoises from Jun. 5 to Sep. 9, 1998, in Haro Strait ($48^{\circ}35'N$, $123^{\circ}16'W$), which lies between southern Vancouver Island, BC, and the San Juan Islands, WA. This waterway is approx.

20 km long, 2.5–8 km wide, and up to 360 m deep. Dall's porpoises are common in this region, occurring typically in groups of one to seven individuals, with a median group size of two (Willis & Miller 1998). Little is known about their social structure, however, groups are generally small and fluid in composition (Jefferson 1987, 1991; Miller 1990).

As with most cetaceans (Schaeff, in press), many aspects of the mating system are unknown; however, the life history and reproductive biology of these cetaceans offer some insight. Most females produce a single dependent offspring each summer, and enter estrus within a month of parturition (Newby 1982; Kasuya & Jones 1984; Ferrero & Walker 1999). Calving peaks in the summer, lasting approx. 6 wk (Jefferson 1989; Ferrero & Walker 1999). In our study region, male–female pairs form following the onset of calving in mid-July, with almost all newly calved females found in association with an adult male (P. M. Willis, pers. obs.). Males appear to enter a stage of 'rut' when females are beginning estrus, increasing in body mass, testes weight, and sperm production (Newby 1982). Males are larger than females, have several prominent secondary sexual characteristics, and have small testes relative to their body size (Newby 1982; Kasuya & Jones 1984; Jefferson 1990; Ferrero & Walker 1999). These features suggest a male mating strategy characterized by contest competition and a low copulatory frequency (Ralls 1977; Newby 1982; Kenagy & Trombulak 1986; Jefferson 1990). As in other cetaceans (Schaeff, in press), there is no evidence of male parental care.

Observation and Categorization of Study Animals

We collected data between 08:00 and 20:00 hours from a 4.7-m Zodiac inflatable boat. Opportunities for underwater observation are limited due to the small size and mobility of these species, and the low clarity of local waters. Therefore, we collected data when animals surfaced to breathe. Sexually mature males are distinguishable from other age/sex classes in the field due to their larger size and prominent secondary sexual characteristics (Jefferson 1990). Because sexually mature females are difficult to distinguish at sea from sub-adults of either sex (Jefferson 1990), we relied on the presence of a newborn calf to identify them. This criterion restricted data sampling of male–female pairs to the postpartum breeding season. As calves first appeared in the study region during the third week of July in 1997 and 1998 (P. M. Willis, unpubl. data), we chose Jul. 15

to represent the onset of the breeding season in our analyses.

We observed individual adult males in association with either another adult male (hereafter referred to as 'male–male pair'), or a newly calved female (male–female pair). Pairs were defined operationally as two individuals separated by over 30 body lengths, or within 30 body lengths of additional individuals, for no more than one surfacing run (a rapid succession of breaths). We restricted observations to pairs, both to control for the effect of group size on male behavior, and to optimize data collection, as sampling feasibility declines substantially with group size.

Predictions

As mate guarding necessitates monitoring female movements, maintaining proximity to her, and defending against extra-pair copulation attempts, we predicted that

1. male–female pairs will be more stable over time than male–male pairs,
2. members of male–female pairs will maintain closer inter-animal distances than those of male–male pairs,
3. males will surface in greater synchrony with females than with males,
4. males paired with females will approach their partner more often than leave her,
5. males paired with females will approach their partner more often than will males paired with other males,
6. males paired with females will respond aggressively to other adult males, and
7. male–female pairs will affiliate with (join) other individuals less often than will male–male pairs.

We assume here a total evidence approach. While not all predictions necessarily exclude alternate hypotheses, considered together they may permit us to interpret our findings as more or less parsimonious with mate guarding.

Surfacing to breath is costly to a deep-diving animal because it competes temporally with foraging, and other important behaviors, at depth. Therefore, dive duration should be optimized (Kramer 1988; Schreer & Kovacs 1997; Thompson & Fedak 2001). Larger diving animals, including cetaceans, have greater diving capabilities and undertake longer dives than do smaller ones, both among and across species (Westgate et al. 1995; Schreer & Kovacs 1997; Martin & Smith 1999; Noren & Williams 2000; Baird et al. 2005). Adult male Dall's porpoises are

5–10% longer and 20% heavier than adult females (Kasuya 1978; Newby 1982; Ferrero & Walker 1999; Ohizumi et al. 2003), and appear to pursue longer periods at depth (P. M. Willis, unpubl. data). To test the hypothesis that males trade-off guarding with time at depth, we predicted that guarding males would undertake shorter duration dives than would males paired with other males.

Focal Animal Sampling and Event Recording

As individuals vary in the shape and pigmentation of the dorsal fin (Jefferson 1990), as well as in other morphological features, we were able to track focal individuals over successive dives. Focal individuals were not identified across sampling sessions, allowing for the possibility that an individual was followed more than once. However, we believe resampling was unlikely due to the abundance of animals and the diversity of animals observed. Upon encountering a pair, one/the adult male was assigned focal status, and a focal sampling session ('follow') initiated.

During a follow, we recorded every surfacing event, to the nearest second, of each member of the pair onto microcassette. When they surfaced within 5 s of each other (minimizing estimate error), we recorded inter-animal distance (in focal body lengths), and the position and orientation of the focal animal relative to its partner. We categorized positions as: 'ahead' – surfacing anterior to the midline of the long axis of the partner, 'behind' – surfacing posterior to the midline, and 'flanking' – surfacing intersecting the midline. Orientations were categorized as: 'toward' – a surfacing with a bearing convergent with the long axis of the partner, 'away' – a surfacing with a non-parallel, non-convergent bearing, and 'parallel' – a surfacing with a bearing not noticeably deviating from either 0° or 180° relative to the long axis of the associate. Ambiguous or missed observations were recorded as 'unknown.' Sampling continued for as long as possible; i.e. until the pair separated, joined other individuals, were lost (i.e. not seen for over 10 min), or until extenuating circumstances (e.g. nightfall, sea conditions) precluded data collection. The age/sex class of joining individuals could not always be ascertained; however, the presence or absence of adult males was noted where possible.

We also recorded the occurrence of 'agonistic events,' characterized by pair encounters with other individuals involving sudden, very active behavior occurring at or just below the water surface. Events

were defined by (1) erratic, non-directional movements, (2) predominantly 'rooster-tailing' (a high-speed surfacing accompanied by a characteristic splash; see Houck & Jefferson 1999) and 'fast surfacing' (Jefferson 1987) surfacing behavior, (3) subsurface splashing and upwelling, (4) close-proximity chases, and (5) aerial behaviors (the protrusion of the tail flukes, head, or body out of the water); very atypical behavior for Dall's porpoises (Jefferson 1987, 1990; P. M. Willis, pers. obs.). Events were considered terminated upon the resumption of typical, 'slow rolling' (Jefferson 1987) surfacing behavior. Focal data collection was interrupted during these events due to our inability to consistently track the focal animal; however, we recorded event duration, the number of extra-pair individuals, the presence or absence of extra-pair adult males, the persistence or dissolution of the original pair following the event, and opportunistic data as to the sequence of events.

Statistical Analyses and Variable Definition

All analyses were carried out using SAS statistical software (version 8.2; SAS Institute, 2001). Analyses of focal follow data were restricted to sessions yielding at least 10 min of continuous data. Session duration, inter-animal distance, and dive duration data were \log_{10} -transformed to approximate normal distributions. All p-values are one-tailed except where noted.

We used general linear model procedures, with pair type as the main effect, to test whether males paired with females yielded longer sessions, maintained closer distances, and undertook shorter dives than those paired with other males. Inter-animal distance and dive analyses included focal identity as the subject to accommodate repeated measures. As distance values within a surfacing run are not independent, inter-animal distances were averaged across observations within individual runs, and the averages analyzed as the dependent variable. A dive was defined as two consecutive breaths more than 30 s apart, whereas lesser intervals (usually in series) constituted a surfacing run. (Cetaceans typically take several breaths in short succession at the surface between long dives; cf. Watson & Gaskin 1983.) The 30-s delimiter was adopted based on inter-breath interval data obtained previously from porpoises in the same region, and which had a bimodal distribution approaching zero at 30 s (P.M. Willis, unpubl. data).

As an additional investigation of pair stability across pair types, we classified sessions by duration

(either < or \geq 10 min), and also by outcome (pair separated or not), and used the Fisher's exact test to test whether male-female pairs persisted longer, and separated less, than male-male pairs.

To further characterize male dive behavior, we also calculated focal male dive rate (dives/h), excluding periods of agonistic behavior or missing observations, and examined whether dive rate differed across pair types, using the two-sample t-test for unequal variances. As follows were initiated independent of the stage of focal dive cycle, we added 0.5 dives per follow to correct for the bias in rate underestimation with follow duration (without this correction, underestimate bias is greater in shorter follows; however, the same analysis without correction yields qualitatively similar results).

To test whether males were more synchronous with, and more often approached, female than male partners; and whether they more often approached females than left them, we used logistic regression models for binary outcomes with the Williams scale option to adjust for overdispersed data. Focal surfacings occurring within 5 s of a partner's were categorized as 'synchronous,' otherwise they were categorized as 'asynchronous'; and the per-session frequency of surfacings of each type compared across pair types. For approach analyses, we created a new variable, 'posor,' from tandem position and orientation measures, with categories of 'approach,' 'leave,' and 'neutral.' An 'approach' was defined by joint position and orientation measures of behind-parallel, behind-towards, flanking-towards, or ahead-towards; whereas a 'leave' corresponded to ahead-parallel, ahead-away, flanking-away, or behind-away; and flanking-parallel defined 'neutral.' Pairwise comparisons were carried out via contrast tests.

Analysis of male-male aggression was carried out by classifying follows by the presence or absence of agonistic events, and testing for an association with pair type, using the Fisher's exact test. Similarly, we tested for lower extra-pair affiliation among male-female pairs by classifying sessions by whether joining occurred or not, and using the Fisher's exact test.

Results

We followed a total of 87 pairs, of which 24 male-male, and 18 male-female, yielded at least 10 min of continuous focal data. Although approximately equal numbers of male-male and male-female follows were initiated during the breeding season ($n = 18$ male-male vs. $n = 24$ male-female, $\chi^2 = 0.857$,

Table 1: Results of generalized linear and logistic regression models testing the effect of pair type on male Dall's porpoise behavior, for focal sessions ≥ 10 min

Variable	Test-statistic	p
Follow duration	$F_{1,40} = 13.06$	<0.001
Inter-animal distance	$F_{1,40} = 95.32$	<0.001
Synchrony	$\chi^2_1 = 26.49$	<0.001
Approaches	$\chi^2_1 = 4.50$	0.018
Dive duration	$F_{1,39} = 11.15$	0.001

$df = 1$, $p = 0.355$), of these, significantly fewer male–male ($n = 3$) than male–female ($n = 18$) follows exceeded 10 min (Fisher's exact test, $p < 0.001$; see also 'Seasonal effect,' below).

Pair Stability

Male–female pairs yielded significantly longer-duration follows than did male–male pairs (Table 1, Fig. 1a). Similarly, male–female pairs also yielded significantly more sessions of at least 10 min duration (18 of 24) than did male–male pairs (24 of 63; Fisher's exact test, $p = 0.002$). Only one male–female pair was observed to separate compared with eight observed separations of male–male pairs, however, this difference was not significant (Fisher's exact test, $p = 0.227$; Fig. 2a).

Inter-animal Distance and Male Synchrony

Males paired with females both maintained significantly closer distances, and surfaced in synchrony significantly more often, than did males paired with other males (Table 1, Fig. 1b,c).

Male Approaches

Focal males approached female partners significantly more often than male ones (Table 1, Fig. 2d). Within male–female pairs, the proportion of male approach, leave, and neutral surfacings differed significantly ($\chi^2 = 28.90$, $df = 2$, $p < 0.001$), with males approaching more often than leaving, although this difference was marginally non-significant ($\chi^2 = 2.41$, $df = 1$, $p = 0.060$).

Agonistic Events

Six agonistic events occurred during follows of male–female pairs, whereas none occurred during male–male pair follows (Fisher's exact test, $p < 0.001$; Fig. 2b). Extra-pair individuals numbered

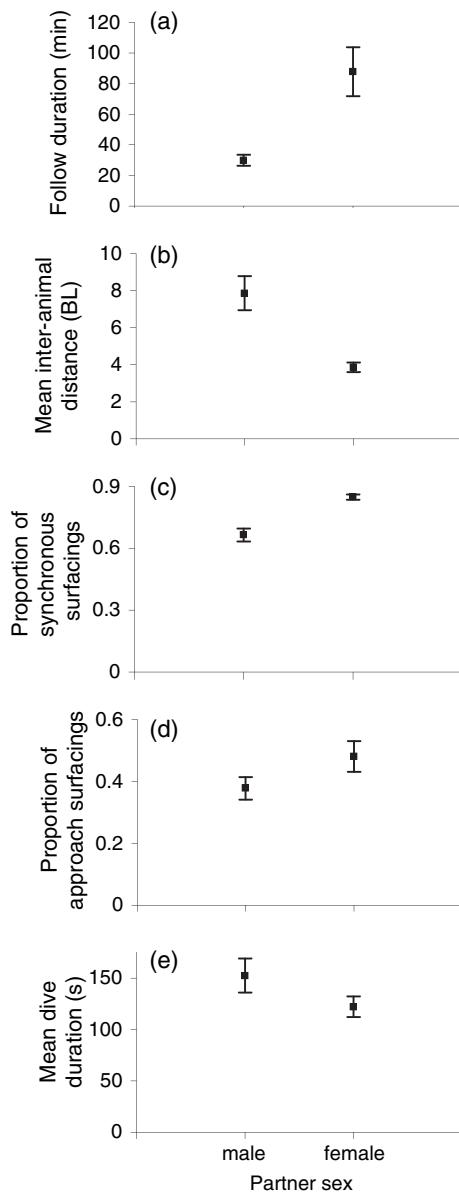


Fig. 1: The effect of partner sex on (a) follow duration, (b) mean inter-animal distance, (c) proportion of surfacings synchronous with partner, (d) proportion of surfacings approaching partner, and (e) mean dive duration; for follows ≥ 10 min. For informative purposes, untransformed and unadjusted data ($\bar{x} \pm SE$) are displayed, averaged across follows ($n = 24$ male partner, $n = 18$ female partner; except in (e), where male partner $n = 23$). Inter-animal distance and dive duration values represent $\bar{x} \pm SE$ of averaged follow values. For statistical analyses, see text. BL = body lengths

between one and three, and always included at least one adult male. Although the identity, age, and sex of individuals were often indiscernible upon surfacing due to heavy water spray, males were often observed interacting directly, chasing each other and

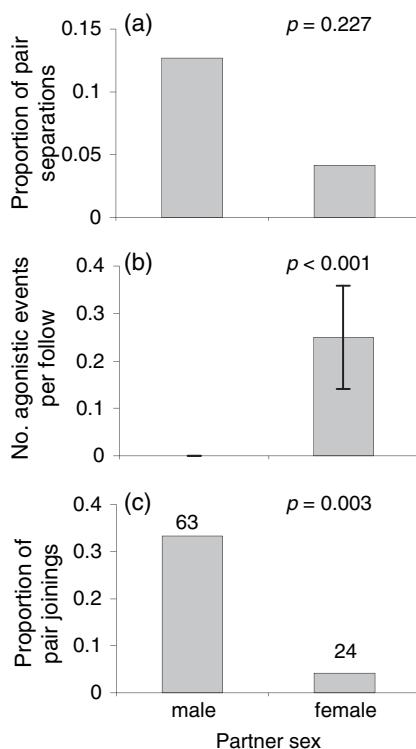


Fig. 2: The effect of partner sex on (a) proportion of pair separations, (b) number of agonistic events/follow, and (c) proportion of pair joinings with other individuals. Numbers over bars are number of follows (same for a, b, and c)

surfacing in close proximity. The female and calf also engaged in high-energy surfacings. The calf was sometimes observed in what appeared to be distress, wriggling forcefully at the surface, and on one occasion was flung out of the water, apparently hit from below. During momentary respites and following termination of the event, the focal male was commonly positioned medially relative to the female and the extra-pair male(s). Events lasted between 1 and 12 min. In five instances the original pair remained intact following the event; in the sixth case the focal animal was lost, and the pair status undetermined.

Joining Events

Male-female pairs joined other individuals only once (a sub-adult), significantly less often than did male-male pairs, which joined one to four individuals in a third of follows (Fisher's exact test, $p = 0.003$; Fig. 2c). The age/sex class of joining individuals was not consistently determined; however, male-male pairs joined one or more adult males on five occasions.

Male Dive Behavior

Males undertook significantly shorter dives when paired with females than when paired with other males (Table 1, Fig. 1e). They also had a significantly higher dive rate when paired with females (26.1 dives/h) than when paired with other males (18.3 dives/h; two-tailed t-test, $t = 2.04$, $p = 0.011$).

Seasonal Effect

As males largely ceased associating for more than fleeting periods upon the onset of breeding, only 3 of 18 sessions initiated during this time exceeded the 10 min duration criterion of some of the analyses, thus confounding sex with season. For example, if individuals became more synchronous in their diving as the summer progressed, independent of sex, then the observed differences between pair types may reflect the bias toward male-male pair data early in the study, and male-female data late. To address the possible influence of an unmeasured seasonal effect, we conducted a posteriori comparisons of male-male behavior across season, as well as male behavior across pair type, using analyses not limited by the 10 min criterion. If some unmeasured seasonal influence were driving the observed patterns, then male-male pairs should exhibit concordant changes as the season progresses. We examined whether male-male pairs sampled during the breeding season yielded more longer-duration (≥ 10 min) sessions, separated less, and affiliated with others less, than those sampled prior to breeding, using the Fisher's exact test.

None of the seasonal predictions were supported. Male-male pairs yielded significantly fewer long duration (≥ 10 min) follows during the breeding season than they did pre-breeding (3/18 vs. 21/45; Fisher's exact test, $p = 0.024$). They also separated more during breeding, although this difference was not significant (4/18 vs. 4/45; Fisher's exact test, $p = 0.154$). Neither did they join other individuals significantly less often during breeding, as predicted by the seasonal hypothesis (4/18 vs. 17/45; Fisher's exact test, $p = 0.188$).

Discussion

This study provides strong behavioral evidence of mate guarding by male Dall's porpoises during the breeding season. Male-female pairs were very stable, in contrast to the ephemeral nature of male-male associations. The close proximity, surfacing

synchrony, and approach behavior of males partnered with females all suggest that they are actively attempting to maintain their association with females, while their participation in agonistic events, and low affiliation, with other adult males suggest they are acting to reduce female extra-pair copulations and increase their own assurance of paternity.

Mate guarding appears to be an uncommon male mating tactic in cetaceans, potentially because the dispersal and mobility of females make this tactic relatively uneconomical (Connor et al. 2000a; Schaeff, in press). This may explain why bottlenose dolphin females are predominantly accompanied by pairs or larger alliances of males, rather than individuals (Wells et al. 1987; Connor et al. 1992; Moors 1997) – attempts to increase paternity assurance may typically be economical only in the context of an alliance (Connor et al. 2000b). The factors facilitating Dall's porpoise mate guarding, which likely exceeds several hours, and possibly days, are unknown. In mammals, the timing of copulation with respect to ovulation affects fertilization success (Gomendio et al. 1998). Therefore, the length and synchrony of estrus, and the predictability of ovulation, should influence the occurrence and intensity of mate guarding (Gomendio et al. 1998; Brotherton & Komers 2003). These reproductive parameters are largely unknown for Dall's porpoises, however, like other odontocetes (Whitehead & Mann 2000), females appear to be spontaneous multiovulators, capable of ovulating multiple times during the breeding season until conception (Newby 1982). If females are receptive for long periods relative to the duration of the breeding season, or males are unable to predict the timing of ovulation, extended mate guarding may be favored (Gomendio et al. 1998; Brotherton & Komers 2003). One or both of these conditions may partially explain the rarity of unguarded, newly calved females in the present study.

It has been suggested that male physical size may be important in sequestering female bottlenose dolphins (Connor et al. 2000b). In Dall's porpoises, the larger body, thoracic hump, and caudal peduncles of males may confer strength and maneuverability conducive to female coercion or defense. We were unable to observe whether males behave aggressively toward their female partners. However, male-female pairs were typically isolated from other individuals, and guarding by male Dall's porpoises, as in male bottlenose dolphins (Connor et al. 2000b; Watson 2005), may involve both sequestering (the use of force directed at females to deter extra-pair

matings) as well as aggression directed towards competing males. Perhaps importantly, females are constrained by their calves, likely affording males easier access and defense. Unlike most other cetaceans, female Dall's porpoises give birth yearly, and are attending to the limited movements and suckling demands of their vulnerable calves during estrus. It would be interesting to determine whether non-parous, receptive females are less often or less intensely guarded, although such differences could reflect females' freedom from the burden of calves, or males' preference for older females, or other factors. Although few data on Dall's porpoise group composition are available, interestingly, newly calved females elsewhere are usually identified either alone, with other female-calf pairs, or in larger groups (Kasuya & Jones 1984; Jefferson 1987; Miller 1989). This suggests that there may be some ecological component(s) unique to the study region favoring mate guarding.

Males largely ceased associating extensively, at least as pairs, upon the onset of the breeding season, possibly in response to competition for mates. Consequently, some of our analyses suffered from the partial confounding of sex with season, allowing for the possibility that an alternative, seasonal influence underlay the observed differences in male behavior. However, the decrease in male-male affiliation at the onset of breeding reflects a departure from, rather than a convergence upon, the behavior patterns of guarding males. Were a seasonal effect responsible, male-male pairs should have exhibited greater stability, lower extra-pair affiliation, and fewer separations during the breeding season than before; rather, they exhibited the opposite, or comparable, patterns. It is not possible to fully discount the role of a seasonal variable unrelated to guarding in contributing to some of the observed differences in male behavior. However, given the full battery of predictions, and the absence of any a-priori potential seasonal factor(s) predicted to influence male behavior in the manners observed, we interpret our findings as most parsimoniously consistent with mate guarding.

The close association of a male with a fertile female may serve a variety of other, non-exclusive functions (reviewed for avian species in Gowaty & Plissner 1987; Birkhead & Möller 1992). Close attendance may serve to increase male sexual access (Gowaty & Plissner 1987). Some bottlenose dolphin consortships, where males neither appear to sequester females, nor contest nearby males (Moors 1997), may represent male attempts to respond to

copulation opportunities. In addition to protecting their paternity through guarding, male Dall's porpoises may also be seeking to increase their sexual access (e.g. displaying towards females). The small testes of male Dall's are indicative of a low copulatory frequency (Jefferson 1990), suggesting that, while associations may concomitantly increase male sexual access, paternity assurance is likely sought primarily through guarding rather than through frequent copulation. The mutual pursuit of copulation opportunities and female defense may also occur in escorting or consorting males of other cetacean taxa (Connor et al. 1992, 1996; Clapham 1996; Watson 2005). In some taxa, close attendance to a female may reflect parental investment (Birkhead & Möller 1992); however, male parental care appears absent in cetaceans (Connor et al. 2000a; Schaeff, in press). Moreover, investment in parental care does not predict male avoidance or aggression toward other males, and thus is unlikely to be responsible for the patterns observed here.

Our focus is on male behavior; however, as guarding may be expected to influence female fitness, females should significantly affect the occurrence and intensity of guarding (Jormalainen 1998; Harari et al. 2003). While male Dall's porpoises are acting to maintain their associations with females, females may also benefit from, and facilitate, guarding. Male harassment in other species can be very costly for unguarded females (e.g. Lovell-Mansbridge & Birkhead 1998; Davis 2002; Endo & Doi 2002) and expensive to resist (e.g. Watson et al. 1998; Jormalainen et al. 2001). Guarding may offer female Dall's porpoises refuge from harassment, possibly increasing foraging efficiency, reducing risk of injury, and/or increasing suckling and protection of their calves. Females may also benefit from guarding if contest competition results in high quality mates, relaxing selection on females for mate choice. However, guarding is unlikely to confer only benefits to females. Guarded females and their calves appear to risk injury from the aggressive interactions of contesting males in close proximity, suffering from at least occasional blows. Depending on the extent of female control over guarding, guarding may also significantly constrain female mate choice. Female bottlenose dolphins and humpback whales sometimes resist consorting attempts (Tyack & Whitehead 1983; Connor et al. 2000b); whether female Dall's similarly resist is unknown. However, prior to the present study, one of us (P. M. Willis) observed a female and calf apparently fleeing an agonistic event, traveling at high speed for several minutes. Future studies

will benefit from incorporating the study of female behavior, as the occurrence and intensity of guarding likely reflects the balance of sexual conflict, with each sex trading off the benefits of guarding with the costs.

Male Dall's porpoises guard individual females for several hours, and possibly days. Mate guarding may therefore comprise a large amount of a male's time during the breeding season, competing with other activities important to survival and reproduction. Guarding in other animals, including other large mammals, is often associated with a reduction in foraging effort, although empirical evidence of a trade-off is limited (Cuthill & Macdonald 1990; Westneat 1994; Alberts et al. 1996; Sparkes et al. 1996; Komdeur 2001). The shorter dive times of guarding males relative to non-guarders suggests a trade-off between time spent at foraging depth and guarding. The cost of undertaking shorter dives may be partially offset by their higher dive rate. However, guarding males are nonetheless likely suffering reduced foraging efficiencies, due to the decrease in the ratio of time spent at foraging depth, to time spent in the ascent and descent phases of a dive. It is possible that males are able to compensate for shorter periods at depth by increasing their feeding rate, or expending less energy. However, if monitoring of the female and potential rivals competes temporally with the detection and capture of prey, which seems likely, foraging efficiency at depth may be compromised. In addition, guarding males appear to incur energetic costs through increased expenditure in chasing and repelling challengers; in other taxa, such costs can be substantial (e.g. Low 2005).

Guarding in other large mammals is often associated with substantial decreases in male weight and condition (Poole 1989; Komers et al. 1994; Alberts et al. 1996; Setchell & Dixson 2001; Pelletier 2005). The increase in male Dall's porpoise body mass at the onset of female estrus may support guarding effort by buffering any energetic deficit and consequent decline in condition over the breeding period. If males vary in phenotypic quality, it is possible that only superior condition males can afford the loss of condition associated with guarding (e.g. McElligott et al. 2003; Pelletier 2005), perhaps other males pursue other reproductive tactics. Future studies of Dall's porpoises may be able to document changes in individual male condition over the course of the breeding season through photogrammetric analysis of the convexity of the dorsal hump, formed from the underlying thoracic epaxial muscle mass (Jefferson 1990), which appears greatest at the onset of

breeding (Newby 1982). With such efforts, combined with observations over longer periods and including both sexes, and with the addition of genetic analyses of paternity, future studies will be able to shed considerable light on this unusual cetacean mating system, and further identify the costs and trade-offs affecting the occurrence and intensity of mate guarding.

Acknowledgements

Thanks to R. W. Baird for valuable input throughout the project. We also thank A. Fraser and D. Witt for technical assistance; B. Hanson, S. Hazlitt, P. Miller, and several field assistants for field support; B. Crespi, D. Lank, and R. Ydenberg for assistance with project design and analyses; and Seacoast Expeditions, 5-Star Charters, Washington State Bureau of Land Management, and Roche Harbor Resort for other assistance in the field. We thank Tom Jefferson and two anonymous reviewers for helpful comments on the manuscript. P.M.W. was supported by a NSERC Canada Postgraduate Scholarship and a Simon Fraser University Graduate Fellowship. Financial support was received from the Exploration Fund, Mountain Equipment Co-op, the PADI Foundation; and NSERC Canada grant A6869 to L.M.D. Approval for animal research issued by the Simon Fraser University Animal Care Committee (project no. 514B), the US National Marine Fisheries Service (permits 873 and 1437), and the Canadian Department of Fisheries and Oceans.

Literature Cited

- Alberts, S. C., Altmann, J. & Wilson, M. L. 1996: Mate guarding constrains foraging activity of male baboons. *Anim. Behav.* **51**, 1269–1277.
- Baird, R. W., Hanson, M. B. & Dill, L. M. 2005: Factors influencing the diving behaviour of fish-eating killer whales: sex differences and diel and interannual variation in diving rates. *Can. J. Zool.* **83**, 257–267.
- Birkhead, T. R. 1979: Mate guarding in the magpie *Pica pica*. *Anim. Behav.* **27**, 866–874.
- Birkhead, T. R. & Möller, A. P. 1992: *Sperm Competition in Birds: Evolutionary Causes and Consequences*. Academic Press, New York.
- Birkhead, T. R. & Möller, A. P., eds. 1998: *Sperm Competition and Sexual Selection*. Academic Press, New York.
- Brotherton, P. N. M. & Komers, P. E. 2003: Mate guarding and the evolution of social monogamy in mammals. In: *Monogamy: Mating Strategies and Partnerships in Birds, Humans, and Other Mammals* (Reichard, U. H. & Boesch, C., eds). Cambridge Univ. Press, Cambridge, pp. 42–58.
- Chuang-Dobbs, H. C., Webster, M. S. & Holmes, R. T. 2001: The effectiveness of mate guarding by male black-throated blue warblers. *Behav. Ecol.* **12**, 541–546.
- Clapham, P. J. 1996: The social and reproductive biology of humpback whales: an ecological perspective. *Mammal. Rev.* **26**, 27–49.
- Connor, R. C., Smolker, R. & Richards, A. F. 1992: Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proc. Natl. Acad. Sci. USA* **89**, 987–990.
- Connor, R. C., Richards, A. F., Smolker, R. A. & Mann, J. 1996: Patterns of female attractiveness in Indian Ocean bottlenose dolphins. *Behaviour* **133**, 37–69.
- Connor, R. C., Read, A. J. & Wrangham, R. 2000a: Male reproductive strategies and social bonds. In: *Cetacean Societies: Field Studies of Dolphins and Whales* (Mann, J., Connor, R. C., Tyack, P. L. & Whitehead, H., eds). Univ. of Chicago Press, Chicago, pp. 247–269.
- Connor, R. C., Wells, R. S., Mann, J. & Read, A. J. 2000b: The bottlenose dolphin: social relationships in a fission-fusion society. In: *Cetacean Societies: Field Studies of Dolphins and Whales* (Mann, J., Connor, R. C., Tyack, P. L. & Whitehead, H., eds). Univ. of Chicago Press, Chicago, pp. 91–126.
- Cothran, R. D. 2004: Precopulatory mate guarding affects predation risk in two freshwater amphipod species. *Anim. Behav.* **68**, 1133–1138.
- Cuthill, I. C. & Macdonald, W. A. 1990: Experimental manipulation of the dawn and dusk chorus in the blackbird *Turdus merula*. *Behav. Ecol. Sociobiol.* **26**, 209–216.
- Davis, E. S. 2002: Female choice and the benefits of mate guarding by male mallards. *Anim. Behav.* **64**, 619–628.
- Endo, A. & Doi, T. 2002: Multiple copulations and post-copulatory guarding in a free-living population of sika deer (*Cervus nippon*). *Ethology* **108**, 739–747.
- Ferrero, R. C. & Walker, W. A. 1999: Age, growth, and reproductive patterns of Dall's porpoise (*Phocoenoides dalli*) from the central North Pacific ocean. *Mar. Mamm. Sci.* **15**, 273–313.
- Gomendio, M., Harcourt, A. H. & Roldán, E. R. S. 1998: Sperm competition in mammals. In: *Sperm Competition and Sexual Selection* (Birkhead, T. R. & Möller, A. P., eds). Academic Press, New York, pp. 667–756.
- Gowaty, P. A. & Plissner, J. H. 1987: Association of male and female American robins (*Turdus migratorius*) during the breeding season: paternity assurance by sexual access or mate-guarding? *Wilson Bull.* **99**, 56–62.
- Harari, A. R., Landolt, P. J., O'Brien, C. W. & Brockmann, H. J. 2003: Prolonged mate guarding and sperm

- competition in the weevil *Diaprepes abbreviatus* (L.). *Behav. Ecol.* **14**, 89–96.
- Houck, W. J. & Jefferson, T. A. 1999: Dall's porpoise *Phocoenoides dalli* (True, 1885). In: *Handbook of Marine Mammals*, Vol. 6: The Second Book of Dolphins and Porpoises (Ridgway, S. H. & Harrison, R., eds). Academic Press, New York, pp. 443–471.
- Jefferson, T. A. 1987: A study of the behaviour of Dall's porpoise (*Phocoenoides dalli*) in the Johnstone Strait, British Columbia. *Can. J. Zool.* **65**, 736–744.
- Jefferson, T. A. 1989: Calving seasonality of Dall's porpoise in the eastern North Pacific. *Mar. Mamm. Sci.* **5**, 196–200.
- Jefferson, T. A. 1990: Sexual dimorphism and development of external features in Dall's porpoise *Phocoenoides dalli*. *Fish. Bull. US* **88**, 119–132.
- Jefferson, T. A. 1991: Observations on the distribution and behavior of Dall's porpoise (*Phocoenoides dalli*) in Monterey Bay, California. *Aquat. Mamm.* **17**, 12–19.
- Jormalainen, V. 1998: Precopulatory mate guarding in crustaceans – male competitive strategy and intersexual conflict. *Q. Rev. Biol.* **73**, 275–304.
- Jormalainen, V., Merilaita, S. & Riihimäki, J. 2001: Costs of intersexual conflict in the isopod *Idotea baltica*. *J. Evol. Biol.* **14**, 763–772.
- Kasuya, T. 1978: The life history of Dall's porpoise with special reference to the stock off the Pacific coast of Japan. *Sci. Rep. Whales Res. Inst.* **30**, 1–63.
- Kasuya, T. & Jones, L. L. 1984: Behavior and segregation of the Dall's porpoise in the northwestern North Pacific Ocean. *Sci. Rep. Whales Res. Inst.* **34**, 107–128.
- Kenagy, G. J. & Trombulak, S. C. 1986: Size and function of mammalian testes in relation to body size. *J. Mamm.* **67**, 1–22.
- Komdeur, J. 2001: Mate guarding in the Seychelles warbler is energetically costly and adjusted to paternity risk. *Proc. R. Soc. Lond. B* **268**, 2103–2111.
- Komers, P. E., Messier, F. & Gates, C. C. 1994: Plasticity of reproductive behaviour in wood bison bulls: when subadults are given a chance. *Ethol. Ecol. Evol.* **6**, 313–330.
- Kramer, D. L. 1988: The behavioral ecology of air breathing by aquatic animals. *Can. J. Zool.* **66**, 89–94.
- Lovell-Mansbridge, C. & Birkhead, T. R. 1998: Do female pigeons trade pair copulations for protection? *Anim. Behav.* **56**, 235–241.
- Low, M. 2005: The energetic cost of mate guarding is correlated with territorial intrusions in the New Zealand stitchbird. *Behav. Ecol.* **17**, 270–276.
- Martin, A. R. & Smith, T. G. 1999: Strategy and capability of wild belugas, *Delphinapterus leucas*, during deep, benthic diving. *Can. J. Zool.* **77**, 1783–1793.
- McElligott, A. G., Naulty, F., Clarke, W. V. & Hayden, T. J. 2003: The somatic cost of reproduction: what determines reproductive effort in prime-aged fallow bucks? *Evol. Ecol. Res.* **5**, 1239–1250.
- Miller, E. J. 1989: Distribution and Behavior of Dall's Porpoise (*Phocoenoides dalli*) in Puget Sound, Washington. MSc thesis, Univ. of Washington, USA.
- Miller, E. J. 1990: Photo-identification techniques applied to Dall's porpoise (*Phocoenoides dalli*) in Puget Sound, Washington. *Rep. Int. Whal. Comm. Spec. Iss.* **12**, 429–437.
- Moors, T. L. 1997: Is a 'menage a trois' Important in Dolphin Mating Systems?: Behavioral Patterns of Breeding Female Bottlenose Dolphins. MSc thesis, Univ. of California, USA.
- Newby, T. C. 1982: Life History of Dall Porpoise (*Phocoenoides dalli*, True 1885) Incidentally Taken by the Japanese High Seas Salmon Fishery in the Northwestern North Pacific and Western Bering Sea, 1978 to 1980. PhD thesis, Univ. of Washington, USA.
- Noren, S. R. & Williams, T. M. 2000: Body size and skeletal muscle myoglobin of cetaceans: adaptations for maximizing dive duration. *Comp. Biochem. Physiol. A* **126**, 181–191.
- Ohizumi, H., Kuramochi, T., Kubodera, T., Yoshioka, M. & Miyazaki, N. 2003: Feeding habits of Dall's porpoises (*Phocoenoides dalli*) in the subarctic North Pacific and the Bering Sea basin and the impact of predation on mesopelagic micronekton. *Deep-Sea Res.* **50**, 593–610.
- Pelletier, F. 2005: Foraging time of rutting bighorn rams varies with individual behavior, not mating tactic. *Behav. Ecol.* **16**, 280–285.
- Poole, J. H. 1989: Announcing intent: the aggressive state of musth in African elephants. *Anim. Behav.* **37**, 140–152.
- Ralls, K. 1977: Sexual dimorphism in mammals: avian models and unanswered questions. *Am. Nat.* **111**, 917–938.
- SAS Institute 2001: The SAS system for Windows, version 8.2. SAS Institute, Cary, NC.
- Saeki, Y., Kruse, K. C. & Switzer, P. V. 2005: Physiological costs of mate guarding in the Japanese beetle (*Popillia japonica* Newman). *Ethology* **111**, 863–877.
- Schaeff, C. M. in press: Courtship and mating behavior. In: *Reproductive Biology and Phylogeny of Cetacea, Whales, Porpoises and Dolphins* (Miller, D. L., ed.). Science Publishers, Enfield, NH. In press.
- Schreer, J. F. & Kovacs, K. M. 1997: Allometry of diving capacity in air-breathing vertebrates. *Can. J. Zool.* **75**, 339–358.
- Setchell, J. M. & Dixson, A. F. 2001: Circannual changes in the secondary sexual adornments of semi-free-ranging male and female mandrills (*Mandrillus sphinx*). *Am. J. Primatol.* **53**, 109–121.
- Setchell, J. M. & Wickings, E. J. 2006: Mate choice in male mandrills (*Mandrillus sphinx*). *Ethology* **112**, 91–99.

- Sparkes, T. C., Keogh, D. P. & Pary, R. A. 1996: Energetic costs of mate guarding behavior in male stream-dwelling isopods. *Oecologia* **106**, 166–171.
- Thompson, D. & Fedak, M. A. 2001: How long should a dive last? A simple model of foraging decisions by breath-hold divers in a patchy environment. *Anim. Behav.* **61**, 287–296.
- Tyack, P. & Whitehead, H. 1983: Male competition in large groups of wintering humpback whales. *Behaviour* **83**, 132–154.
- Watson, J. J. 2005: Female mating behavior in the context of sexual coercion and female ranging behavior of bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia. PhD thesis, Georgetown Univ., Washington, DC.
- Watson, A. P. & Gaskin, D. E. 1983: Observations on the ventilation cycle of the harbour porpoise *Phocoena phocoena* (L.) in coastal waters of the Bay of Fundy. *Can. J. Zool.* **61**, 126–132.
- Watson, P. J., Arnqvist, G. & Stallmann, R. R. 1998: Sexual conflict and the energetic costs of mating and mate choice in water striders. *Am. Nat.* **151**, 46–58.
- Wells, R. S., Scott, M. D. & Irvine, A. B. 1987: The social structure of free-ranging bottlenose dolphins. In: *Current Mammalogy*, Vol. 1 (Genoways, H., ed.). Plenum Press, New York, pp. 247–306.
- Westgate, A. J., Read, A. J., Berggren, P., Koopman, H. N. & Gaskin, D. E. 1995: Diving behavior of harbour porpoises, *Phocoena phocoena*. *Can. J. Fish. Aquat. Sci.* **52**, 1064–1073.
- Westneat, D. F. 1994: To guard mates or go forage: conflicting demands affect the paternity of male red-winged blackbirds. *Am. Nat.* **144**, 343–354.
- Whitehead, H. & Mann, J. 2000: Female reproductive strategies of cetaceans: life histories and calf care. In: *Cetacean Societies: Field Studies of Dolphins and Whales* (Mann, J., Connor, R. C., Tyack, P. L. & Whitehead, H., eds). Univ. of Chicago Press, Chicago, pp. 219–246.
- Willis, P. M. & Miller, P. J. 1998: Shore observations of Dall's porpoise and their behavior with respect to environmental parameters, including a tidal front. In: *Abstracts of the World Marine Mammal Science Conference*, Monte Carlo, Monaco, January 20–25. Society for Marine Mammalogy, San Francisco, CA, p. 50.