



The ecological costs to females in a system with allied sexual coercion



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ARTICLE INFO

Article history:

Received 16 August 2015

Initial acceptance 21 October 2015

Final acceptance 18 January 2016

MS. number: A15-00709R

Keywords:

bottlenose dolphin
centroid
habitat use
mating system
ranging
sexual coercion
sexual conflict
spatial ecology
Tursiops

Sexual coercion results from extreme conflict over mating. As a male strategy to overcome female resistance, coercion can impose fitness costs on females. Among mammals, most cases involve single males or temporary coalitions, with allied aggression towards females being rare. Among Shark Bay bottlenose dolphins, *Tursiops cf. aduncus*, male alliances harass, guard and consort with females to obtain mating access, which has known physical costs to females. However, the behavioural and ecological costs of sexual coercion to females remain largely unexplored. Given the importance of individual differences in ranging and habitat use for dolphin foraging ecology, social networks and fitness, we hypothesized that male coercion also imposes ecological costs on females. Using 25 years of longitudinal data, we examined how adult male presence relates to female space use, and we found that females ($N = 32$) altered their ranging when associating with adult males but also when they were cycling. Additionally, females reduced the use of their primary (preferred) habitat when with males, but cycling had no effect. Ranging shifts were slightly greater for males than for females when they were together, but only for females did this alter their spatial ecology. While it is also possible that males follow fertile females and/or that females move to avoid males, the well-documented coercive mating system suggests that males, as part of their coercive mating tactics, sequester females to areas that females would not otherwise occupy. Our results show that in a coercive mating system, males can alter females' basic behavioural ecology, and suggest that males spatially sequester individual females via allied consortships.

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Sexual coercion, an extreme example of sexual conflict, is defined as when males, at some cost to females, direct 'force' or the 'threat of force' towards females to increase their chances of mating when females are fertile, and to decrease females' chances of mating with other males (Smuts & Smuts, 1993). Coercion, an adaptive male strategy to overcome female resistance to mating and monopolize breeding opportunities, is an important force in sexual selection (Clutton-Brock & Parker, 1995) and can potentially even lead to divergence and speciation (Panhuis, Butlin, Zuk, & Tregenza, 2001). Furthermore, direct costs to females due to male sexual aggression can be severe and include injury (Hiruki, Stirling, Gilmartin, Johanos, & Becker, 1993; Le Boeuf & Mesnick, 1991), increased energy expenditure (Watson, Arnqvist, & Stallmann, 1998), increased mortality (Réale, Bousset, & Chapuis, 1996), physiological stress (Muller, Kahlenberg, Thompson, & Wrangham, 2007) and decreased reproductive success (Gay, Eady, Vasudev, Hosken, & Tregenza, 2009; Hiruki et al., 1993; den Hollander &

Gwynne, 2009; Ojanguren & Magurran, 2007; Rossi, Nonacs, & Pitts-Singer, 2010; Takahashi & Watanabe, 2010). None the less, because documenting such fitness costs is challenging, particularly in wild, long-lived animals, some researchers have examined the behavioural and ecological costs females experience as a result of male coercion, which may or may not have consequences for fitness. For example, studies documenting changes in movement and ranging (e.g. Grevy's zebra, *Equus grevyi*: Sundaesan, Fischhoff, & Rubenstein, 2007), activity patterns (e.g. southern elephant seals, *Mirounga leonina*: Galimberti, Boitani, & Marzetti, 2000; mollies, *Poecilia* spp.: Heubel & Plath, 2008; humpback whales, *Megaptera novaengliae*: Cartwright & Sullivan, 2009; guppies, *Poecilia mexicana*: Köhler et al., 2011) and sociality (e.g. guppies, *Poecilia reticulata*: Darden, James, Ramnarine, & Croft, 2009; Darden & Watts, 2012) suggest that male coercion influences important aspects of female behavioural ecology and probably fitness. Yet among these studies, few have examined the impact that males have on female behaviour or fitness when they act collectively (i.e. coalitionary or allied aggression), perhaps because, outside of humans (Rodseth & Novak, 2009), some nonhuman primates (chimpanzees, *Pan troglodytes*: Connor & Vollmer, 2009; Muller, Kahlenberg, & Wrangham, 2009; Watts, 1998; baboons, *Papio*: Noë, 1992; spider

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monkeys, *Ateles*: Link, De Fiore, & Spehar, 2009) and some bottlenose dolphin (*Tursiops* spp.) populations (Connor, Smolker, & Richards, 1992a; Connor & Vollmer, 2009), allied males rarely direct aggression towards females.

In several long-term studies of bottlenose dolphins, researchers have documented a sexually coercive mating system in which adult males form long-term, stable alliances (Connor & Vollmer, 2009) of variable size (Connor, Heithaus, & Barre, 2001; Owen, Wells, & Hofmann, 2002; Wells, 1991; Wiszniewski, Brown, & Möller, 2012) that cooperate to consort and mate with individual, primarily cycling, females (Connor, Richards, Smolker, & Mann, 1996; Connor et al., 1992a; Smolker, Richards, Connor, & Pepper, 1992). Consortships are typically initiated by aggressive herding behaviours such as biting, hitting, chasing and threat displays or captures, followed by intermittent aggression throughout the consortship (Connor & Smolker, 1996; Connor et al., 1992a). Among Indian Ocean bottlenose dolphins, *Tursiops* cf. *aduncus*, in Shark Bay, Australia, preliminary evidence suggests that allied males influence female ecology. Previous work found that females spend more time in deeper water and less time in shallow water when in consortships (Watson-Capps, 2005). Although the benefits or costs of this shift are not fully understood, changes in depth use suggest that male coercion may affect female spatial ecology.

Shark Bay dolphin spatial ecology has been previously described in some detail. Individuals exhibit bisexual philopatry and have large, overlapping home ranges that are stable through time (Tsai & Mann, 2013). Habitat use is influenced by both predator (tiger shark, *Galeocerdo cuvier*) and prey distributions on large and small spatial scales (Heithaus & Dill, 2002, 2006), meaning even small shifts in space use could have potentially serious ecological outcomes for dolphins. However, such shifts probably have the greatest impact on female ecology given that females exhibit habitat-specific foraging specializations (Mann & Sargeant, 2003; Mann et al., 2008, 2012; Sargeant, Mann, Berggren, & Krützen, 2005; Sargeant, Wirsing, Heithaus, & Mann, 2007), have smaller home ranges and lower habitat use diversity compared to males (Patterson, 2012). For example, some females specialize in a foraging tactic known as sponging, which involves the use of marine sponges as tools and only occurs in the deep channels where sponges and appropriate prey are found (Mann et al., 2008; Patterson & Mann, 2011; Sargeant et al., 2007). Sponger females could be severely affected if consorting males move them away from the channel habitat. In contrast, individual males and alliances have much larger home ranges and greater habitat use diversity (Patterson, 2012; Randić, Connor, Sherwin, & Krützen, 2012), which probably relates to their need to roam the bay to find and maintain access to fertile females. Thus, not only is efficient space use inherently important for survival, but the observed variation among individuals and among sexes is an explicit representation of individual ecological needs.

When considering that male and female space use must coalesce during consortships, three scenarios are possible. First, it may be that males spatially sequester females by consorting with them in accordance with their alliance's space use. Here one would expect substantial ecological costs to females, and no such costs to males. Second, it may be that males spatially sequester females to some extent, but also partially adjust their alliance's space use to temporarily match that of fertile females. Here one would expect ecological costs to both sexes, the magnitude of which would depend on the relative space use shifts for each sex. Finally, it may be that males do not spatially sequester females and instead temporarily adjust their alliance's space use to match that of their targeted mate's range (i.e. males go where the fertile females are and follow them around). Here one would expect males, but not females, to suffer an ecological cost.

Given the aggressive nature of consortships, the first or second scenario, both of which impose some ecological costs on females, seems most likely. Thus, we hypothesize that males present an ecological cost to adult females by altering female space use, specifically, their ranging and habitat use. If alliances sequester females to their own, much larger home ranges, females will probably be far from their core home range area and their preferred foraging habitats. Accordingly, we predicted that (1) females would be farther from their home range core (i.e. the centroid) when they were with more than one male compared to when they were not, and that (2) females would use their preferred habitat less when they were with more than one male compared to when they were not. However, this does not preclude consortships from affecting male space use. Nevertheless, given that males have larger home ranges and greater habitat use diversity than females, even if males do alter their space use during consortships, we expected the relative impact of consortships on spatial ecology to be greater for females than for males. Thus, we predicted that, (3) if males do experience space use shifts during consortships, such shifts in both ranging and habitat use would be relatively greater for females than for males when the sexes were together. Female-biased space use shifts would suggest that females suffer an ecological cost in this coercive mating system.

METHODS

Study Population and Site

Our study population consists of individually recognised wild Indian Ocean bottlenose dolphins (*T. cf. aduncus*) residential to Shark Bay, Western Australia (Mann, Connor, Barre, & Heithaus, 2000; Tsai & Mann, 2013). As part of the Shark Bay Dolphin Research Project (SBD RP), researchers have collected behavioural, demographic, reproductive, ecological, social and genetic data on more than 1800 dolphins since 1984. Individuals are distinguished using standard dorsal fin identification techniques (Würsig & Würsig, 1977). Sex is determined by the presence of a dependent calf, views of the genital area (Smolker et al., 1992), and in a few cases, DNA (Krützen, Sherwin, Berggren, & Gales, 2004). Age is determined from known or estimated birthdates (if seen as a calf), physical and behavioural characteristics (Mann & Smuts, 1999), and/or the presence and degree of ventral speckling (Krzyższyk & Mann, 2012).

Our main study site is a 300 km² area of the eastern gulf of Shark Bay (25°47'S, 113°43'E) within a UNESCO World Heritage Site, and as a result, remains relatively pristine with low human impact. Habitat in the study area, as defined by Patterson (2012), consists of six distinct types (average depths reported relative to datum): 'channel' (7.13 m): with a substrate of rock, shell and coral debris; 'deep open' (6.56 m): with a mixed sand, silt and clay substrate; 'sea grass beds' (2.00 m): with continuous sea grass coverage (predominantly *Amphibolis antarctica* and more sparsely *Posidonia australis*); 'sand flats' (−0.11 m): with continuous sand coverage; and two edge habitats: 'deep ecotone': the transition zone between a shallow habitat (sea grass beds or sand flats) and deep habitat (channel or deep open); 'shallow ecotone': the transition zone between two shallow habitats (sea grass beds and sand flats). Relative habitat availability was calculated as the proportion of the study area with coverage of that habitat type (Patterson, 2012).

Data Collection

Survey records

Data collection for the SBD RP consists primarily of observational, boat-based records. For this study, data were drawn from

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