



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



Megan M. Wallen<sup>a,\*</sup>, Eric M. Patterson<sup>a</sup>, Ewa Krzyszczyk<sup>a</sup>, Janet Mann<sup>a,b</sup>

<sup>a</sup> Department of Biology, Georgetown University, Washington, D.C., U.S.A.

<sup>b</sup> Department of Psychology, Georgetown University, Washington, D.C., U.S.A.

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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

\* Correspondence: M. M. Wallen, Department of Biology, Georgetown University, 406 Reiss Science Bldg, Washington, D.C. 20057-1229, U.S.A.

E-mail address: [mmw89@georgetown.edu](mailto:mmw89@georgetown.edu) (M. M. Wallen).

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 km<sup>2</sup> 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

surveys, which are opportunistic sightings of dolphins, conducted from 1988 to 2012. A survey began when observers were close enough to identify or photograph individuals. Scan sampling (Altmann, 1974; Mann, 1999) is used for the first 5 min of a survey to determine group composition and activity. Group membership was determined using a 10 m chain rule, where all individuals within 10 m of another group member were considered to be in association (Smolker et al., 1992). Predominant group activity was recorded as the behaviour that at least 50% of the group members engaged in during the scan in the first 5 min. Spatial data (latitude and longitude) were also collected during each survey, to later be used in classifying each survey's habitat based on the aforementioned habitat classifications. If an individual had more than one survey sighting in a day, we restricted our data set to include only the last survey point per individual per day to reduce spatial and temporal correlation.

#### Female cycling

Male interest in females is expected to vary with female reproductive status. Thus, we included female cycling status (whether or not she was cycling) as the first factor in our study. Bottlenose dolphins are seasonally polyoestrous with an estimated 6-month peak cycling period prior to the ~12-month pregnancy (O'Brien & Robeck, 2012; Schroeder, 1990). Accordingly, we assigned cycling periods as the 6-month period before the start of known pregnancies (from known births). However, this definition biases observations against females who have produced no or few surviving calves, or have long intervals between nursing calves since they are potentially fertile during periods when no pregnancies are confirmed by a birth. Consequently, we included additional time periods in which a female could be cycling, based on the period (1) from the female's 12th birthday (when 42.4% of first births occur, while 22.0% occur at age 11,  $N = 59$  adult females where age of first birth was known) until her first known pregnancy, and (2) 1 year prior to the weaning date for calves that nursed beyond the age of 4 years, the average weaning age (average interbirth interval between surviving calves is 4.7 years; Mann et al., 2000). This method overestimates cycling periods (increasing the risk of type II error), but since females go through several nonconceptive cycles per year, it conservatively accounts for potential fertile periods. Since most of our data (76% of surveys) were collected during the 6 months prior to the November peak births/conceptions (Mann et al., 2000), we have adequate coverage over periods of cycling. Females were considered to be noncycling if they were (1) pregnant or (2) nursing a calf that was at least 12 months from its weaning date. Thus, our cycling factor has two levels: cycling and not cycling. Females under the age of 12 years were excluded from analysis.

#### Male presence

Individual pairs or trios of males (first-order alliances) typically have very strong bonds, with half-weight coefficients of association (COAs) as high as 0.8–1.0 (Connor et al., 1992a, 1992b, 2011). Second-order alliances are composed of two or more first-order alliances (Connor & Vollmer, 2009) with COAs ranging from 0.24 to 0.67 (Connor & Krützen, 2015), and third-order alliances are composed of second-order alliances and their close male associates with slightly lower COAs ranging from 0.10 to 0.17 (Connor et al., 2011). Because males are found so frequently with their alliance partners and very rarely with nonpartners, as a proxy for consortships we used the presence of more than one adult male in a survey. Males were considered to be adult at 12 years of age or older (Cheal & Gales, 1992). Thus, we used male presence as the second factor in our study, having two levels: >1 male present, in which more than one adult male was present in the survey (representing the

minimal unit for allied coercion), and males absent, in which no adult males were present in the survey. Here, single-male associations were omitted. Males and females are monomorphic and there is no evidence that a single male can monopolize a female. Although allied aggression towards females is frequently observed (Connor et al., 1996; Scott, Mann, & Watson-Capps, 2005), aggression by a lone adult male towards an adult female has never been observed in 28 years of study and 3467 h of focal observation on 127 adult females (Mann, n.d.; Scott et al., 2005). Furthermore, associations between single males and single or multiple females are rare (see Results, Table 1). Nevertheless, for a subset of females in our sample, we included a third level for the male factor: surveys in which a single male was present with at least one adult female (see Supplementary Material).

#### Data Analysis

Cycling status (cycling or not cycling) and adult male presence (males absent, 1 male present, >1 male present) were included as factors in our analyses. Since reproductively successful females spend most of their adult life pregnant and/or lactating, not cycling, and rarely in association with males (Gibson & Mann, 2008), we considered the baseline state to be surveys when females were not cycling and males were absent. We conducted a similar analysis on males to examine whether their behaviour is affected by the presence of a female. Males spend most of their time with each other (Connor et al., 1992a, 1992b, 2011) and not in consortships, so we considered the male baseline state to be surveys when no adult females were present (females absent) and there was at least one additional adult male present. The male baseline was compared to surveys where males were with at least one female (cycling or noncycling), resulting in a single factor with three levels for the male analysis (no females, only noncycling female(s) present, and only cycling female(s) present). Dolphins were included in the sample if they had a minimum of six survey sightings on different days in each factor level (e.g. cycling female with males; one point possible for each habitat based on habitat availability), and the same females ( $N = 32$ ) and males ( $N = 73$ ) were used for all analyses (the smaller sample size for females reflects the additional cycling restriction). A subset of 11 females with adequate survey data was analysed using the single-male comparison (results shown in the Supplementary Material). For all analyses regardless of overall significance tests, we conducted a priori contrasts between all three levels of male presence.

#### Ranging

As a measure of core ranging we calculated a baseline centroid for each individual by averaging all GPS locations from survey records in the baseline state. Centroids for males and females were

**Table 1**

Proportion of sightings per individual per factor level used in the full data set (32 females,  $N = 4611$  surveys, 7004 female sightings)

	Sighting proportion	
	Not cycling	Cycling
♀ or ♀♀	0.715	0.551
♀, ♂	0.021	0.015
♀, ♂♂	0.040	0.114
♀♀, ♂	0.073	0.071
♀♀, ♂♂	0.152	0.248

♀: 1 adult female present; ♀♀: >1 adult female present; ♂: 1 adult male present; ♂♂: >1 adult male present. For analysis, surveys with one female and one male were lumped with those that had more than one female and one male to form the one-male factor level.



calculated for their baseline state excluding sightings from all other factor levels. To examine whether ranging differed with cycling status and male presence (for females) or with female presence including cycling status (for males), we compared the distances between the baseline centroid and each survey GPS record within each factor level using permutation tests with dolphin ID as a blocking factor. While somewhat counterintuitive, we also compared the distance of the baseline centroid to each baseline survey point used in its calculation, as this serves as the best measure of expected distance from the baseline centroid if there were no effect of male presence or cycling status. We then compared the distances from the baseline for each sex when they were found together to determine whether females and males differentially shifted in ranging. The average number of surveys ( $\pm$ SD) per female per factor level was  $102.75 \pm 103.24$  (not cycling, males absent),  $21.13 \pm 14.50$  (not cycling, >1 male present),  $46.31 \pm 38.96$  (cycling, males absent) and  $26.41 \pm 17.32$  (cycling, >1 male present). The average number of surveys ( $\pm$ SD) per male per factor level was  $43.69 \pm 17.57$  (females absent),  $66.97 \pm 53.15$  (cycling female(s) present) and  $15.38 \pm 8.70$  (only noncycling female(s) present).

To further understand how cycling and male presence influence female ranging, and how female presence influences male ranging, we also calculated the average pairwise distance between all sightings for each individual within each factor level (hereafter average ranging distance). We examined the effect of cycling, male presence, and their interaction (for females), and the effect of female presence (for males) on this average ranging distance using permutation tests.

#### Habitat use

After spatially intersecting our survey sightings with the six habitat classifications, we quantified individual preferred (hereafter primary) habitat use using selection ratios. Selection ratios indicate habitat selection by an individual while correcting for habitat availability. Selection ratios were calculated as the proportional use of a habitat divided by the proportional availability of that habitat (Manly, McDonald, Thomas, McDonald, & Erickson, 2002). Values greater than one indicate selection above that expected based on availability, values less than one indicate selection below that expected based on availability, and values equal to one indicate selection in accordance with availability. We ranked each individual's baseline habitats (1°, 2°, 3°, etc.) in descending order by their selection ratio, with the primary (1°) habitat having the highest value. Habitat use shifts were examined as a function of cycling status and male presence (for females) and female presence, including cycling status (for males), using distanced-based, permutation MANOVAs with dolphin ID as a blocking factor. In this analysis the last-ranked habitat (6°) was dropped since otherwise the response would be linearly dependent.

Because many dolphins, mostly females, specialize in habitat-specific foraging tactics (Mann et al., 2008; Patterson & Mann, 2011; Sargeant et al., 2005, 2007), we examined primary habitat use alone with permutation independence tests. We expected the primary habitat to be the most important habitat for females and likely the most affected by male presence. We then compared the primary habitat use selection ratio for each sex when they were found together to determine whether females and males differentially changed use of their primary habitat. The average number of surveys ( $\pm$ SD) per female per factor level was  $99.94 \pm 103.97$  (not cycling, males absent),  $20.13 \pm 14.00$  (not cycling, >1 male present),  $44.38 \pm 38.42$  (cycling, males absent) and  $23.78 \pm 15.05$  (cycling, >1 male present). The average number of surveys ( $\pm$ SD) per male per factor level was  $36.89 \pm 17.24$  (females absent),  $57.16 \pm 49.43$  (cycling female(s) present) and  $14.35 \pm 8.25$  (only noncycling female(s) present). See the Interactive Map for a visualization of

habitats in the study area as well as representative male and female spatial data by factor level.

#### Statistical considerations

All of our response variables deviated significantly from normality (all Shapiro–Wilk tests:  $P < 0.01$ ), thus permutation tests were used in all analyses (Anderson, 2001). Permutations (1000 randomizations) were performed using the coin package (Hothorn, Hornik, van de Wiel, & Zeileis, 2006) in R v.3.2.1 (R Core Team, 2015), except for the female habitat and ranging distance analyses, in which custom permutations tests were written using the lme4 package for R (Bates, Maechler, Bolker, & Walker, 2014) to test for interaction (Anderson, 2001). Permutation MANOVAs were performed using the adonis() function in the vegan package for R (Oksanen et al., 2013), which permutes the raw data and calculates a pseudo- $F$  using a multivariate distance measure, here the Bray–Curtis distance. For all analyses, the interactions were tested and tests for main effects were only performed if interactions were determined to be nonsignificant. Significance was set at  $\alpha = 0.05$  for all tests and Bonferroni adjustments were applied where there were multiple contrasts, and the corrected  $P$  values are reported. Female centroid distances were ln transformed to correct for heteroscedasticity (Levene's test:  $P < 0.01$ ), but raw distance values are reported for illustrative purposes.

## RESULTS

#### Female Associations with Males

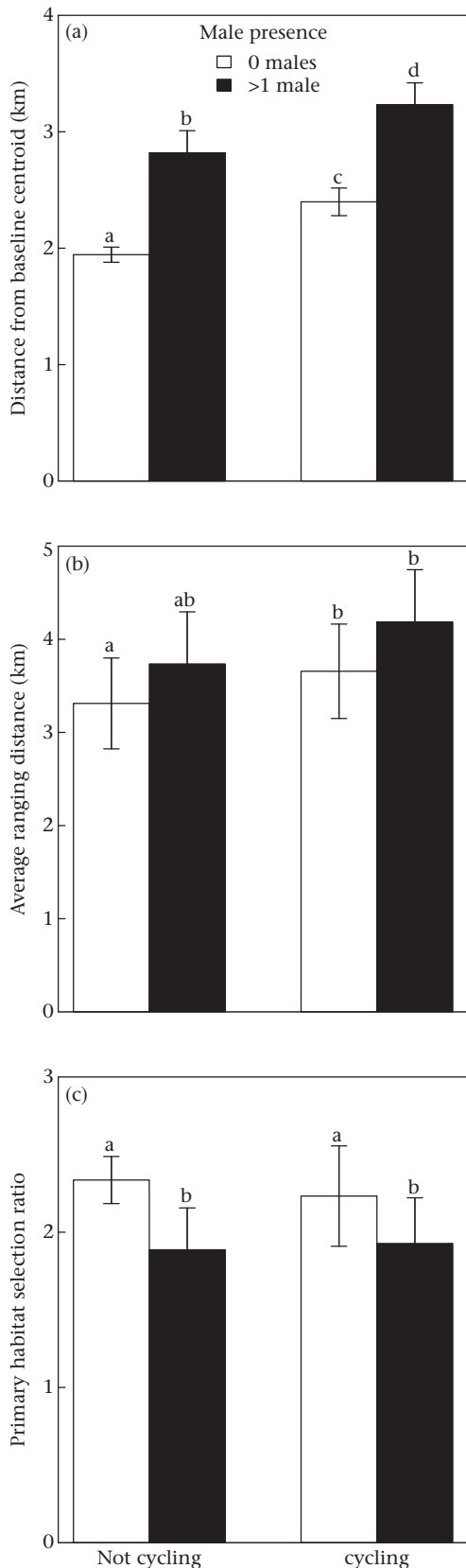
Adult females spent most of their time either alone or with other adult females (Table 1). Females were with more than one male about one-third of the time when cycling, and were very rarely with lone males regardless of reproductive state. These descriptive data provide context for our results.

For all the following analyses, results from the single-male associations were either not significant or largely intermediate between male-absent and multimale associations (see Supplementary Fig. S1, Table S1). As evident from Table 1, instances of single-male associations with females were rare and thus our sample sizes are limited (see Supplementary Material for results and discussion of all single-male associations).

#### Ranging

There was no interactive effect of cycling status and male presence on distance from baseline for female ranging (permutation  $F$  test:  $F_{1,124} = 0.24$ ,  $P = 0.63$ ), so main effects are reported. Both cycling status (permutation  $Z$  test:  $Z = -4.30$ ,  $N = 32$ ,  $P < 0.0001$ ) and male presence ( $Z = -7.08$ ,  $N = 32$ ,  $P < 0.0001$ ) influenced the distance (ln transformed) that a female was found from her baseline centroid. Females were sighted farthest from their baseline centroid when they were with males, and also when they were cycling (Fig. 1a). In contrast, male distances from their baseline centroid were unrelated to female presence or female cycling status (permutation test:  $T_{\max} = 1.63$ ,  $N = 73$ ,  $P = 0.20$ ; Fig. 2a). In comparing male and female distances from their baselines to when there was at least one female and more than one adult male in the group, the distances of each sex to their respective baseline centroids differed (permutation  $Z$  test:  $Z = -2.35$ ,  $N = 32$  females, 73 males,  $P = 0.02$ ), with males being farther from their baseline centroid than females.

Females' average ranging distance was not influenced by an interaction between cycling status and male presence (permutation  $F$  test:  $F_{1,124} = 0.13$ ,  $P = 0.72$ ), so main effects are reported. Both cycling status ( $Z = -2.55$ ,  $N = 32$ ,  $P = 0.009$ ) and male presence



**Figure 1.** Adult female ( $N = 32$ ) (a) distance from the baseline centroid, (b) average ranging distance and (c) primary habitat selection ratios for each combination of cycling and male presence factor levels. Error bars indicate  $\pm 1$  SE. Letters indicate significant differences after Bonferroni adjustments. Distances in (a) were  $\ln$  transformed for analysis but raw distances are shown for illustrative purposes.

( $Z = -3.06$ ,  $N = 32$ ,  $P = 0.003$ ) affected a female's average ranging distance (Fig. 1b). Females had the highest average ranging distance when cycling and when more than one male was present, which was significantly higher than the baseline state only ( $Z = -3.56$ ,  $N = 32$ ,  $P < 0.0001$ ) after a Bonferroni correction (Fig. 1b). However, cycling females without males also had a higher average ranging distance than females in the baseline state ( $Z = -2.85$ ,  $N = 32$ ,  $P = 0.001$ ; Fig. 1b).

Males' overall average ranging distance was influenced by female presence ( $T_{\max} = 5.09$ ,  $N = 73$ ,  $P < 0.0001$ ). Males had the highest average ranging distance when no females were present compared to when noncycling female(s) ( $Z = 4.79$ ,  $N = 73$ ,  $P < 0.0001$ ) and cycling females ( $Z = -2.77$ ,  $N = 73$ ,  $P = 0.005$ ) were present (Fig. 2b). Average male ranging distance was greater when cycling females were present than when only noncycling female were present ( $Z = 3.24$ ,  $N = 73$ ,  $P = 0.002$ ; Fig. 2b).

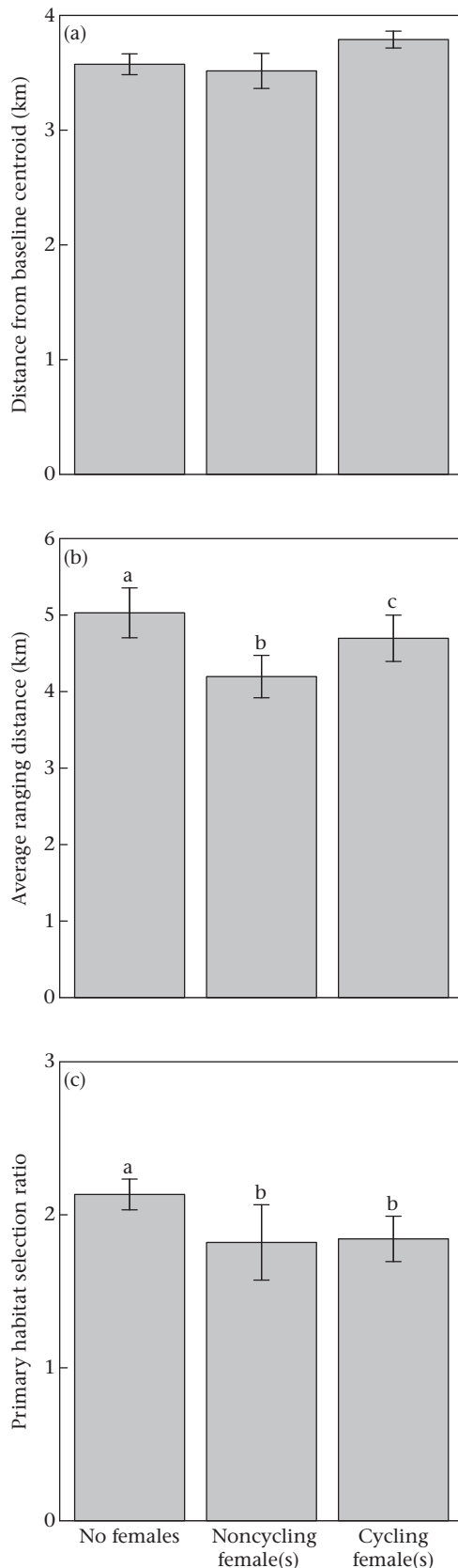
#### Habitat Use

The interaction between male presence and cycling status on overall female habitat use was not significant (Table 2). However, overall female habitat use did change significantly as a function of male presence but not cycling status (Table 2). Per our a priori prediction, we examined the effect of cycling and male presence on female primary habitat alone (Fig. 1c). There was no interaction between cycling status and male presence on primary habitat use (permutation  $F$  test:  $F_{1,124} = 0.44$ ,  $P = 0.53$ ), so only main effects are reported. Consistent with the results from the MANOVA, all females used their primary habitat less when in the presence of more than one male ( $Z = 3.32$ ,  $N = 32$ ,  $P = 0.0003$ ), independent of cycling status, which itself was not significant ( $Z = 0.28$ ,  $N = 32$ ,  $P = 0.78$ ). In the baseline state, females were sighted in their primary habitat 62% of the time, and this decreased by an average of 15% when more than one male was present.

Overall male habitat use changed as a function of female presence (Table 2), as did the primary habitat when analysed alone ( $T_{\max} = 3.54$ ,  $N = 73$ ,  $P = 0.001$ ). Males used their primary habitat less when either cycling or noncycling females were present compared to when no females were present (cycling females:  $Z = -4.25$ ,  $N = 73$ ,  $P < 0.0001$ ; noncycling females:  $Z = 2.59$ ,  $N = 73$ ,  $P = 0.008$ ; Fig. 2c). However, male habitat use did not differ depending on whether they were with cycling females or noncycling females ( $Z = 0.23$ ,  $N = 73$ ,  $P = 0.84$ ). In baseline, males were sighted in their primary habitat 54% of the time, and this decreased by an average of 4% when either cycling or noncycling females were present. In comparing the reduction in primary habitat use between males and females from their baseline to when there was at least one female and more than one adult male in the group, the reduction in primary habitat use did not differ between the sexes ( $Z = 0.54$ ,  $N = 32$  females, 73 males,  $P = 0.58$ ).

#### DISCUSSION

Our findings are consistent with the sexual coercion hypothesis that allied males impose ecological costs on females, in that females experienced space use shifts when in the presence of more than one adult male. Specifically, females were sighted farthest from their baseline centroid, had greater average ranging distances and showed altered habitat use when with more than one male, regardless of cycling status. Interestingly, cycling status alone also affected female ranging in that females had greater ranging distances and were found farther from their baseline when cycling, regardless of male presence. This suggests an overall change in ranging, although not habitat use, during cycling that may be unrelated to mating. Together, our results suggest that allied male



**Figure 2.** Adult male ( $N = 73$ ) (a) distance from the baseline centroid, (b) average ranging distance and (c) primary habitat selection ratios for each factor level. Error bars indicate  $\pm 1$  SE. For distance from baseline centroid (a), there were no significant differences across groups. For average ranging distance (b) and habitat selection ratios (c), letters indicate significant differences after Bonferroni adjustments.

coercion imposes ecological costs on female bottlenose dolphins, but some range shifts may occur outside of consortships when females are cycling.

Males did not experience as great a shift in their spatial ecology during mating contexts as did females. Males were found equally far from their baseline whether or not a female (either cycling or noncycling) was present. However, male average ranging distance decreased when with cycling and noncycling females. This is unsurprising as males are expected to range widely when searching for females, and preliminary data suggest that males have smaller home ranges during peak breeding in the spring (Randić, 2008). When a female was present, male average ranging distance was higher if the female was cycling, which suggests that males (1) match movement of the females they are consorting and/or (2) maintain greater ranging to avoid detection or conflict with other alliances. Both predictions corroborate our finding that female average ranging distance was higher when cycling. While males did alter their overall habitat use and decreased their primary habitat use in the presence of females, this did not depend on a female's cycling status. The lack of a cycling status effect here may indicate that males have imperfect detection of female reproductive states. Females nurse calves for 2.5–9 years and often wean their calf during the next pregnancy (Mann et al., 2000). With such long and variable lactation periods, male ability to detect or predict female fertility is likely imperfect. Males have also been observed to consort noncycling and pregnant females (Connor et al., 1996; Furuichi, Connor, & Hashimoto, 2014), which may be a male-bonding tactic rather than about increasing the likelihood of conceptions per se.

When directly comparing centroid and habitat shifts during sightings of possible mating contexts (i.e.  $>1$  male and  $\geq 1$  female together in surveys), we found that males experienced larger ranging shifts than females, and there was no habitat shift sex difference. However, while the presence of males altered females' normal ranging patterns (Fig. 1a), the same was not true for males when in the presence of females (Fig. 2a); male centroid distance remained constant regardless of female presence (cycling or noncycling). Males typically have larger home ranges than females (Owen et al., 2002; Patterson, 2012; Randić et al., 2012; Sprogis, Raudino, Rankin, MacLeod, & Bejder, 2016; Urian, Hofmann, & Wells, 2009; but see Tsai & Mann, 2013), so any shift they experience probably has less of an impact on their overall space use compared to a similar shift in females. In fact, increased ranging may actually be beneficial for males since the size of their home ranges is associated with their coercive mating tactics (Randić et al., 2012), and alliances tend to range more widely to maximize their search area and access to females (Randić et al., 2012). Furthermore, while both males and females experienced similar primary habitat use shifts in mating contexts, adult males have higher habitat use diversity than adult females (Patterson, 2012), and they do not specialize in foraging tactics nearly as much as females (e.g. Mann & Sargeant, 2003; Mann et al., 2008, 2012; Sargeant et al., 2005), so a shift in primary habitat probably has less of an impact on male foraging than it would for more specialized females.

While males experienced smaller shifts in their spatial ecology when with females, our results clearly demonstrate ranging shifts for females in consortship contexts that probably impose ecological costs. For example, adult female home ranges in Shark Bay average  $51 \text{ km}^2$  (Tsai & Mann, 2013), compared to  $76 \text{ km}^2$  for adult males (Randić et al., 2012). Thus, the average centroid shift of 3 km when cycling and with males reported here would probably place a female near the edge or outside of her home range, if, as a conservative example, a female has a circular home range with an area of  $51 \text{ km}^2$  and a radius of 4 km.

Interestingly, female sightings were farther apart (ranging distance) and farther from their baseline centroid when they were

**Table 2**

MANOVA results for overall female habitat use selection ratios and effects of female cycling status and male presence, and overall male habitat use selection ratios and the effect of female presence, including cycling status

		df	MS	F	R <sup>2</sup> <sub>adj</sub>	P
<b>Females</b>	Cycling	1	0.05	0.66	0.01	0.29
	Male presence	1	0.19	2.33	0.02	<0.01
	Cycling * male presence	1	0.04	0.55	0.00	0.37
	Residual	124	9.85		0.97	
<b>Males</b>	Female presence	2	0.12	1.40	0.01	0.03
	Residual	216	0.09		0.99	

cycling regardless of male presence. Thus, in general, cycling females appear to increase their ranging. For females with dependent calves, additional ranging may be especially costly, which raises the question of why cycling females might increase their ranging behaviour. We propose three possible explanations for increased movement during cycling, all of which warrant further investigation. First, cycling females might increase ranging to avoid detection by allied males. Second, females might increase ranging to avoid consortships with specific alliances (e.g. reduce probability of incestuous matings; see Frère, Krützen, Kopps, 2010) and/or increase the chance of encountering preferred alliances or multiple male partners. Third, as an artefact of our study methods, females might be sighted between consortships after males have already moved them far from their core ranging area. Increased travelling during cycling has been reported in other systems: in Mahale chimpanzees, *Pan troglodytes schweinfurthii*, oestrous females travel greater distances (Hasegawa, 1990) and spend more time moving than their anoestrous counterparts (Matsumoto-Oda & Oda, 1998). In giraffes, *Giraffa camelopardalis*, cycling females tend to locomote more than pregnant females (del Castillo, Bashaw, Patton, Rieches, & Bercovitch, 2005). Lactating Grevy's zebra have elevated speeds compared to nonlactating females, and these females experience the most male harassment (Sundaesan et al., 2007). In black-faced impalas, *Aepyceros melampus petersi*, postparturient females forage in different microhabitats and elevations than preparturient females (Matson, Putland, Jarman, le Roux, & Goldizen, 2007), suggesting finer-scale habitat decisions may indeed be influenced by reproductive status alone. In contrast, in our study, female cycling status influenced average ranging distance and distance from baseline centroid, but not habitat use. This suggests that although females do increase ranging and possibly their home range, they appear to do so in way that maintains their preferred habitat use. Such range shifts are not likely as costly as those experienced in a consortship context.

Females experienced overall habitat use shifts, and importantly a reduction in primary habitat use, when with more than one male. Reduced primary habitat use has direct implications for female foraging behaviour since many females specialize in habitat-specific foraging tactics (Mann et al., 2008; Patterson & Mann, 2011; Sargeant et al., 2005, 2007). For instance, given that spongers are almost never sighted more than 6 km from their channel habitat (Mann & Patterson, 2013), consortship by males almost certainly takes them into unfamiliar habitat outside of their baseline area. In fact, one sponger female in this study reduced her channel habitat use by 36% when she was with males. In such a scenario, habitat and site unfamiliarity may present significant challenges, such as extra search effort to find sponge tools and/or prey, which may alter foraging success (Patterson, Krzyszczyk, & Mann, 2015). Indeed, previous work found that females foraged less during consortships (Watson-Capps, 2005), which could be because they were spending less time in their primary foraging habitat. An examination of group behaviour data from the surveys

used in this study indicates that females have reduced foraging budget in consortship contexts. Foraging was the predominant activity of groups consisting of a female and more than one male only 20% of the time, compared to 32% for groups of females without males. While such a reduction suggests an energy intake cost to females as a result of male coercion, we emphasize that these group behaviour data are not ideal for examining individual female changes in activity budgets (Karniski et al., 2015). Instead, individual focal follow data should provide a more accurate picture of female activity budgets with respect to cycling status and male presence, a topic of our future work.

Together, our results suggest that males spatially sequester females during consortships, from which they may gain several benefits. By sequestering females, males likely affect the ability of females to counter their efforts. For example, on a number of occasions, we have witnessed adult females appearing to 'assist' other females in consortships (see also Connor, Mann, & Watson-Capps, 2006). In these cases, the assisting female may join a group where males are harassing a close associate, and remain in close proximity or even establish physical contact with her. While males may try to separate these females, the females sometimes succeed in leaving the group. By spatially moving females away from their close associates, males might reduce the risk that they will receive aid. Indeed, female social relationships are closely tied to their home ranges (Frère, Krützen, Mann, 2010; Mann et al., 2012), so females displaced from their preferred areas may not have their common female associates available, albeit temporarily.

Another benefit of sequestration is that males may be able to reduce competition from other alliances. Alliances vary in size (Connor et al., 1999; Randić et al., 2012) and can be fiercely competitive, with larger alliances often defeating smaller ones (Connor et al., 1999). Presumably this is why males cooperate in the first place: to increase their ability to maintain exclusive access to a female even though they must share in matings with alliance members. The best tactic for males might be to remove a female from an area where other males are likely to search. Finally, by using coercion within or outside of female cycling periods, males may be acting to increase their own reproductive success, as has been found in chimpanzees (Feldblum et al., 2014).

While our data indicate that male coercion negatively affects female spatial ecology, three alternative, but nonmutually exclusive, explanations are possible. First, females might actually alter their space use when cycling, and males simply follow them in order to gain mating access. As noted above, females of a variety of mammalian species increase their ranging during cycling for many reasons. However, we failed to find an overall effect of cycling on habitat use. Thus for this alternative hypothesis to hold, females would need to specifically alter their preferred habitat use only in the company of males, or, males would need to only follow a female if she is both cycling and in a nonpreferred habitat. While this is certainly possible, we are unaware of any data that support this somewhat unusual scenario. Second, females might shift their space use to avoid males, and thus the ecological shifts represent the costs of a female counterstrategy to male aggression, rather than the cost of coercion itself. While we cannot rule out this possibility, in such a scenario the threat of male coercion would still impose an indirect cost on females if avoidance requires moving away from preferred areas. Finally, rather than experiencing direct costs from sexual coercion, females may be experiencing indirect costs as a result of a male strategy to reduce intrasexual competition via spatial segregation. Since these two explanations result in the same behaviour (females mating with sequestering males, and not other competing males), we are unable to disentangle the root source of these ecological costs. If alliance formation and maintenance is actually a strategy to reduce male competition, particularly



in areas where males have a high encounter rate (Connor & Krützen, 2015; Connor & Whitehead, 2005) and encounters with cycling females are rare, then coalitionary aggression, sequestration and monopolization of individual females may be the best way for males to achieve mating success. Future studies employing focal follow methods on individual females with and without males, in all reproductive states, may prove useful in ruling out these alternative explanations.

Currently, the costs of sexual conflict are not well understood, especially among long-lived mammals where fitness outcomes can take decades to assess (Aloise King, Banks, & Brooks, 2013) and female counterstrategies may be in place (Palombit, 2014). However, our results suggest that in bottlenose dolphins, males have a significant impact on female space use that probably affects foraging behaviour and potentially fitness. Given that female bottlenose dolphins spend weeks or even months in consortships (Connor et al., 1996), these spatial, ecological costs may be long lasting. For reproductively successful females that nurse calves for 3 years or longer and that cycle about every 4–5 years, consortship frequency, and thus the costs of male coercion may be low. However, for females with low calving success, repeated annual consortship events might have more severe negative impacts. As such, the fitness costs of sexual conflict to females in the bottlenose dolphin mating system deserve further study.

Our study contributes to the growing body of literature documenting behavioural costs to coercive mating and provides clear evidence for the costs of allied male aggression in a nonhuman species. In other coercive systems, the threat of male coercion forces female avoidance (e.g. guppies, *P. reticulata*: Darden & Croft, 2008), and even sexual social segregation (e.g. small-spotted catsharks, *Scyliorhinus canicula*: Wearmouth et al., 2012). Male chimpanzees lead females away in consortships, effectively mate guarding (Tutin, 1979). However, all known cases involve single male harassment of females (but see Watts, 1998), and we are unaware of any cases where males engage in stable and long-term cooperation to coerce females as in bottlenose dolphins. Importantly, few studies have looked at the relationship between coercion, female reproductive status and the effects on individual ecology. Such an integrative approach is important for understanding the mechanisms by which coercion can influence female fitness, and ultimately the evolution of mating systems.

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## Supplementary Material

Supplementary material associated with this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2016.02.018>.

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