

Effects of size and sex on the courting success and foraging behaviour of *Embiotoca jacksoni*

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Abstract

To test life-history theory that body size and sex should influence how animals allocate time to foraging *versus* reproductive activities, we measured the effects of size and sex on courting success and foraging behaviour of black surfperch *Embiotoca jacksoni* off Santa Catalina Island, southern California. Observations of focal fish were made while snorkelling, during which the length of each fish (estimated to the nearest cm), total duration of courting encounters and foraging rates were recorded. We made observations during and outside the mating season. Courtship occurred only between pairs and its duration increased with the size of both the male and female. Although males would court females that were smaller or larger than themselves, pairs that were closely matched in size had long courting sessions, whereas those that differed considerably in size courted only briefly. Small fish foraged more than larger fish, both during and outside the mating season. Males and females foraged at similar rates outside of the mating season, but during the mating season males reduced their foraging rates to less than half that seen outside of the mating season, whereas females continued to forage at the same rate. This decrease in foraging rate of males during the mating season was seen in all sizes of males but was proportionally greatest in the largest males. These observations indicate that males trade off time spent on foraging for time spent courting during the mating season, whereas females do not.

KEYWORDS

black surfperch, courting, Embiotocidae, foraging, mating, trade offs

1 | INTRODUCTION

Animals are predicted to allocate energy in a way that optimises the net resource gain and ultimately maximises fitness (Calow, 1985; Depczynski *et al.*, 2007; Hixon, 1981; Perrin & Sibly, 1993). Because time or energy spent on certain activities typically comes at the expense of other activities, trade-offs must be made. For example, for an individual to spend time courting potential mates, it may have to sacrifice time that it could have spent foraging. Optimal foraging theory predicts that in species where males court females, males will minimise time spent gathering food and maximise time spent courting.

Females in non-territorial species are predicted to be foraging time maximisers, as successful production of offspring requires high intake of energy (Hixon, 1987; Hoffman, 1983; Pyke, 1984; Pyke *et al.*, 1977; Schoener, 1971). Thus, in species with a distinct mating season, one might expect to see a reduction in foraging by males during the mating season to allow for greater dedication of time to reproductive activities, whereas females may not alter their foraging activities, or might even increase them. Additionally, individuals of different sizes may allocate time or energy differently because size can influence the probable success of activities like courtship, territorial defence and foraging (Byström *et al.*, 2006; Culp & Scrimgeour, 1993; Markert &

Arnegard, 2007). Studying the behaviour of animals during and outside of the mating season can help clarify the way these tradeoffs are made.

Surfperches (family Embiotocidae) provide excellent opportunities to study trade-offs between foraging and mating because mating behaviour is distinctly seasonal and many species are easy to observe in the field. While several studies on embiotocids have explored mating behaviour (DeMartini, 1988; Froeschke *et al.*, 2007; Shaw & Allen, 1977; Warner & Harlan, 1982) or foraging behaviour (Holbrook *et al.*, 1985; Schmitt & Holbrook, 1984), or both behaviours (Tootell & Steele, 2012), none have empirically evaluated trade-offs between the two behaviours. Typically, the size of an individual affects the success of males at courtship. In some species, males will only court females of similar size (size-assortative courtship) and will only display agonistic behaviour against other males of similar size (DeMartini, 1988; Warner & Harlan, 1982). In other species, males will court females of a wide range of sizes, but courtship is most successful with females of similar size (DeMartini, 1988; Tootell & Steele, 2012). Generally, for the species studied to date, larger males defend territories that contain mating sites and sometimes food, which provides them & to females via mate selection by females (Hixon, 1981; Shaw & Allen, 1977; Warner & Harlan, 1982). Most previous studies of courtship in this family have focused on three species, all of which are smaller than our study species: kelp surfperch *Brachyistius frenatus* Gill 1862, shiner surfperch *Cymatogaster aggregata* Gibbons 1854 and dwarf surfperch *Micrometrus minimus* (Gibbons 1854). Here, we explore courtship and foraging behaviour in the black surfperch *Embiotoca jacksoni* Agassiz 1853 (see also Froeschke *et al.* (2007) for courtship behaviour in this species).

Embiotoca jacksoni is a medium size surfperch that reaches a maximum size of 35 cm total length (L_T ; Miller & Lea, 1972), though typically it is <25 cm L_T in southern California, with a maximum age of 7 years (Froeschke *et al.*, 2007). The peak of the mating season of *E. jacksoni* is in late October to early November and parturition occurs mainly in May and June (Froeschke *et al.*, 2007). Maturity is typically attained at age 1 year at a size of 10 cm standard length (L_S), which is c. 12 cm L_T . Males and females grow at similar rates and the rate of growth in length is fastest during the first 2 years of life. Growth is very slow after age 5 years, at which age fish are c. 22 cm L_T on average (Froeschke *et al.*, 2007). In some locations, larger males defend territories during the mating season and sometimes defend territories containing food and shelter outside of the mating season (Hixon, 1981). In other locations, large males do not defend mating territories (Froeschke *et al.*, 2007). Smaller males and females of all sizes do not defend territories (Hixon, 1981).

Foraging behaviour can change with body size due to changes in ability to collect prey as size increases (Byström *et al.*, 2006). Foraging capabilities of *E. jacksoni* are limited by gape size and the foraging behaviour of this species shifts from indiscriminate picking to more selective foraging as they grow (Schmitt & Holbrook, 1984). Consequently, smaller individuals may consume more prey than larger individuals, but each prey item may be less energetically valuable than those consumed by larger fish (Holbrook *et al.*, 1985). In many species

of fish, searching and handling ability become more refined in larger individuals, which enables specialisation on more valuable prey (Mittelbach, 1981).

To evaluate foraging and courtship behaviour in *E. jacksoni* and the potential trade-off between these behaviours, we quantified these behaviours in the field and made observations within and outside of the mating season. We tested the following hypotheses: (a) foraging rate declines with body size, (b) foraging rate decreases during the mating season, especially for males because they invest more in courtship behaviour, (c) larger fish are more successful in courting, and (d) courtship success is highest for similarly sized pairs.

2 | MATERIALS AND METHODS

This observational study was conducted in Big Fisherman Cove, Santa Catalina Island, California (33° 26' 40" N, 118° 29' 06" W). This site has plentiful shallow, rocky reef habitat that is covered in macroalgae and is used by *E. jacksoni* for foraging and mating. We recorded data both outside of the mating season (during the last week of September and the first week of October 2014) and during the mating season (last week of October through to late November 2014). We did not observe any courtship activity during late September and early October, though Froeschke *et al.* (2007) recorded courtship as early as July at another site with typically cooler water. We assume that the behaviours observed during our study were generally representative of the mating season and outside of it, though observations during other months would be needed to verify that. All observations were made by a single observer while snorkelling in shallow water (< 1.5 m deep) where all behaviours could be easily monitored. All observations were made in the early afternoon to avoid changes in behaviour throughout the day.

Foraging rates were recorded during 2 min long observations of focal fish. During each observation, we recorded the number of bites taken, as well as the sex and size of the fish. Bites were defined as any contact between the mouth and the food source (generally bushy, understory macroalgae). We visually estimated the size (L_T , cm) of each fish with reference to a ruler held close to the fish. The sex of each fish was determined by the presence (male) or absence (female) of a gonopodium on the anal fin.

A total of 120 focal-fish observations were made, with 60 made outside of the mating season and 60 made during the mating season. During each of the two periods, 20 fish were observed in each of three size classes: small, intermediate and large. In each size class, 10 females and 10 males were observed. Outside of the mating season (late September–early October), the three size classes were defined as 5–10, 11–15 and > 15 cm L_T . During the mating season (late October – late November) the size classes were adjusted up slightly to compensate for growth between the two time periods and were 5–12, 13–16 and > 16 cm L_T . These size classes correspond approximately to juveniles, young adults and older adults (Froeschke *et al.*, 2007).

To test whether foraging rate changed with fish size, we first used linear regression of bite rate on L_T . We fit two regression lines: one for the period prior to the mating season and another for during the mating season. Analysis of covariance (ANCOVA) was used to test whether the slopes of the two relationships were similar and whether the average foraging rates differed between the two periods, after accounting for effects of body size. To test for differences in foraging rate between sexes and size classes of fish and evaluate whether these differences were affected by season (mating or not), three-way analysis of variance (ANOVA) was used with the factors size class, sex and season. The data met the assumptions of normality, homogeneity of variances and linearity (in the case of regression). All statistical analyses used SYSTAT 13 (www.systatsoftware.com).

Courtship observations were made during the mating season (late October–November). Data on courtship were gathered by remaining in locations where many *E. jacksoni* were present and at any point a male initiated courting behaviour, the number of seconds that passed until the two fish separated was recorded as the duration of courtship. Courting behaviour in males generally consists of posturing with the mouth pointed down at a c. 45° , flaring the dorsal fin, and orienting the ventral side towards the female. The female will then either respond or swim away. Responses by the female include nudging, circling and positioning with her ventral side facing the male's ventral side. The two will then swim in spirals until they swim to a nearby cave where it is assumed that mating occurs (Froeschke *et al.*, 2007). The actual act of mating has not been observed in *E. jacksoni*; copulation is typically very brief and rarely observed in surfperch species (Carlisle *et al.*, 1960; Nakazono *et al.*, 1981; Warner & Harlan, 1982). We also were unable to observe mating, but we assumed that long courtships were more successful than short ones, as more of the long courtships ended with the pair retreating to a cave, presumably to mate. A total of 150 courtship interactions were observed. Operationally, a courtship interaction was defined as the male exhibiting courting behaviour in close proximity to a female. The size (L_T , cm) of the male and female were visually estimated with reference to a ruler.

The relationship between courtship duration and body size was tested with two separate linear regressions, one for each sex. Such relationships describe overall patterns of size dependence in courtship effort and success. Courtship success may also be influenced by the degree of match or mismatch in body size. How size differences between male–female pairs affected courtship duration was tested with one-way analysis of variance (ANOVA), with absolute difference in size treated as a categorical independent variable. We used this approach rather than regression because the relationship between courtship duration and size differences was non-linear and estimated size differences were restricted to a small set of discrete values (0, 1, 2, 3, 4, 5, 6, 7, or 8 cm) and by using absolute difference in size, this analysis ignored potential asymmetry; e.g., a size difference of 4 cm could correspond to a male courting a female either a female 4 cm larger or smaller than himself. To further explore how size similarity or differences between male–female pairs affected courtship duration, we graphically evaluated how courtship duration was related to size differences expressed as male L_T :female L_T . Here, negative values

occurred when males courted females larger than themselves and positive values when males courted smaller females. Asymmetries could be generated, for example, by either sex preferring to mate with larger members of the opposite sex. In contrast, preference for similar size mates could generate a symmetrical pattern.

Because the fish we observed in this study were not readily recognisable as individuals and plausibly the same individuals remained in the study area from day to day, it is possible that some fish were observed more than once, causing a slight lack of independence in the data. We estimate that approximately 100 individuals were present within our study site on any given day of sampling. Hence, the results of our statistical tests should be interpreted with some caution, though the effect of this non-independence is likely to be small. In general, the data met the assumption of homogeneity of variances for the regressions and ANOVA, but the assumption of normality of the response variable (courtship duration) was not met and the data could not be transformed to meet it. We used regression and ANOVA anyway because these parametric tests are robust to violations of the normality assumption, especially when the assumption of homogeneity of variances is met (Gotelli & Ellison, 2013).

3 | RESULTS

3.1 | Foraging

Smaller fish foraged more frequently than larger fish over the range of sizes observed (5–25 cm L_T ; Figure 1). The decline in foraging rate with length was linear both outside the mating season (regression: $t = 11.1$, $df = 58$, $P < 0.001$, $r^2 = 0.36$) and during it ($t = 8.6$, $df = 58$, $P < 0.001$, $r^2 = 0.30$). The slope of the decline in foraging rate with increasing body length was similar prior to the mating season and during it (ANCOVA: $F_{1,116} = 0.001$, $P > 0.05$; Figure 1). When data from both sexes were pooled together, average foraging rate was 16%

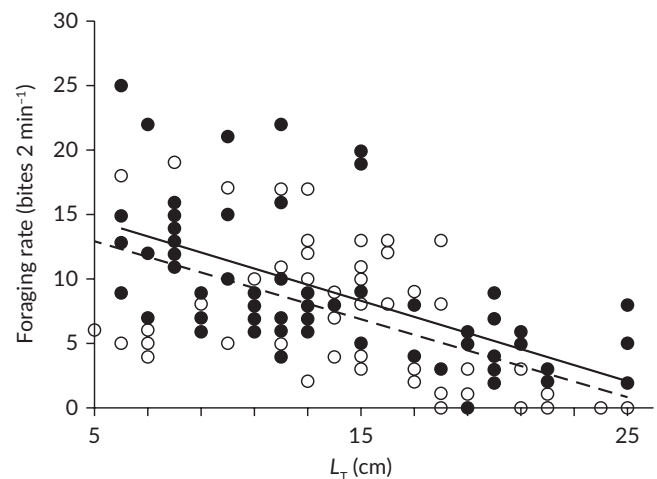


FIGURE 1 Relationships between foraging rate (bites 2 min^{-1}) and total length (L_T) in *Embiotoca jacksoni* prior to the mating season and during the mating season ($n = 60$ focal-fish observations per season). —, Non-mating season ($P < 0.001$, $r^2 = 0.36$); - - - - -, mating season ($P < 0.001$, $r^2 = 0.30$)

lower during the mating season than prior to it, but this difference was not statistically significant (ANCOVA: $F_{1,117} = 2.7$, $P > 0.05$; least-squares adjusted means: 8.86 v. 7.47 bites 2 min^{-1} prior to and during the mating season, respectively; Figure 1).

During the mating season, foraging rates of males decreased, whereas those of females remained indistinguishable from those recorded outside of the mating season (ANOVA: sex \times season interaction: $F_{1,108} = 23.4$, $P < 0.001$; Table 1 and Figure 2). The biggest proportional drop in male foraging rate was seen in large males (L_T 20+ cm), which foraged at only 15% of the rate seen outside the mating season, whereas small and intermediate sized males foraged at c. 38% and 71% of the rate seen outside the mating season, respectively. During the mating season, small, intermediate and large females foraged at 126%, 122% and 82% of the rates recorded prior to the mating season, respectively. These differences in how foraging changed between seasons and among size classes of the two sexes were statistically significant (sex \times size \times season interaction: $F_{2,108} = 4.7$, $P < 0.01$; Table 1).

3.2 | Courtship

Males tended to initiate courtship with females that were similar to their own size (i.e., size-assortative courtship), although there was considerable variation in the size of the females courted by males of a given size (regression: $r^2 = 0.44$, $t = 5.3$, $df = 148$, $P < 0.001$; Figure 3). For example, males courted females as much as 7 cm smaller and 8 cm larger than themselves. Males as small as 9 cm L_T courted females and females as small as 9 cm were courted. In 44% of courtships the female was larger, 43% the male was larger and in 13% the pair were matched in size (L_T to the nearest cm). Only males $>20 \text{ cm } L_T$ were observed defending territories. The maximum size of both males and females involved in courtship was 25 cm; no fish $>25 \text{ cm}$ were seen.

Although courtship initiation was not strongly dependent on similarities in size, courtship duration was. Pairs that were most closely matched in size courted longest. Courtship duration was well predicted by the difference in size between the courting male and female, with courtship duration increasing as the difference in size decreased (ANOVA: $F_{8,141} = 50.4$, $P < 0.001$; Figure 4). It did not appear to matter whether size-mismatched pairs had a male that was larger or a female that was larger, as courtship duration was

TABLE 1 Results of three-way ANOVA testing for differences in foraging rates of *Embiotoca jacksoni* between seasons (mating or not), sex (male or female), and sizes (small, intermediate, or large)

Source	df	MS	F	P
Season	1	100.7	7.3	< 0.01
Sex	1	237.3	17.2	< 0.001
Size	2	733.8	53.3	< 0.001
Season \times sex	1	322.5	23.4	< 0.001
Season \times size	2	22.4	1.6	> 0.05
Sex \times size	2	4.4	0.1	> 0.05
Season \times sex \times size	2	65.3	4.7	< 0.01
Error	108	13.8		

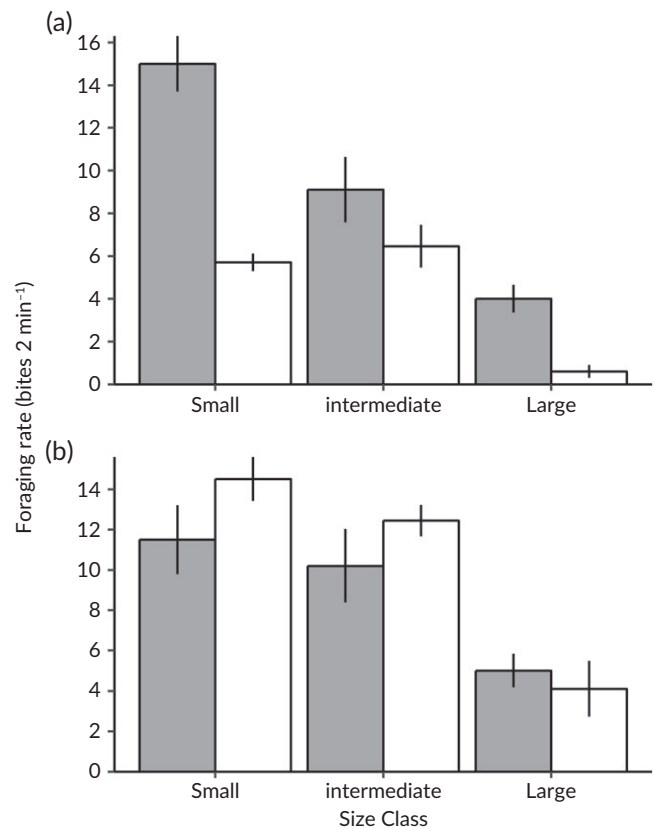


FIGURE 2 Mean (\pm SE) number of bites 2 min^{-1} observation period for three size classes of *Embiotoca jacksoni* (a) prior to the mating season and (b) during the mating season (n = 10 per bar). Size categories: prior to the mating season; small, 5–10 cm total length (L_T); intermediate, 11–15 cm L_T ; large, $> 15 \text{ cm } L_T$; during the mating season: small, 5–12 cm L_T ; intermediate, 13–16 cm L_T ; large, $> 16 \text{ cm } L_T$. ■, Male; □, female

approximately equal in both scenarios (Figure 5). In general, larger males tended to court longer than smaller males ($t = 3.4$, $df = 148$, $P < 0.001$; Figure 6); and larger females also tended to be involved in longer courtships ($t = 2.2$, $df = 148$, $P < 0.05$). Although both relationships were statistically significant, neither predicted much of the

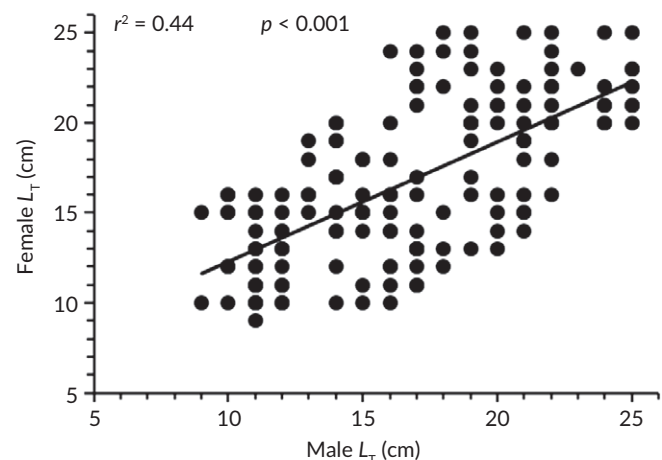


FIGURE 3 Relationship between male and female total length (L_T) of *Embiotoca jacksoni* in courting pairs; n = 150

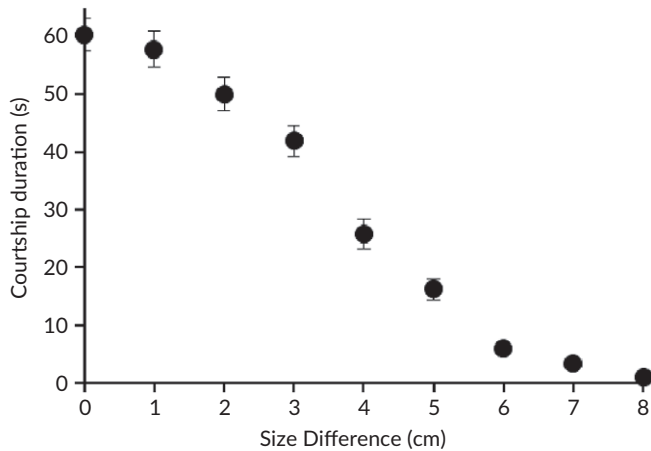


FIGURE 4 Mean (\pm SE) duration of courting encounters for nine classes of total length size difference between male and female *Embiotoca jacksoni*. $n = 20, 25, 26, 18, 22, 16, 18, 4$, and 1 observations for size differences 0, 1, 2, 3, 4, 5, 6, 7, and 8 cm, respectively

variation in courtship duration ($r^2 = 0.07$ and 0.03 for males and females, respectively), presumably because being close in size to the other member of the pair was much more important for successful courtship (Figure 5).

4 | DISCUSSION

Our findings indicate that male and female *E. jacksoni* probably face different costs and benefits of foraging v. courting. Females did not

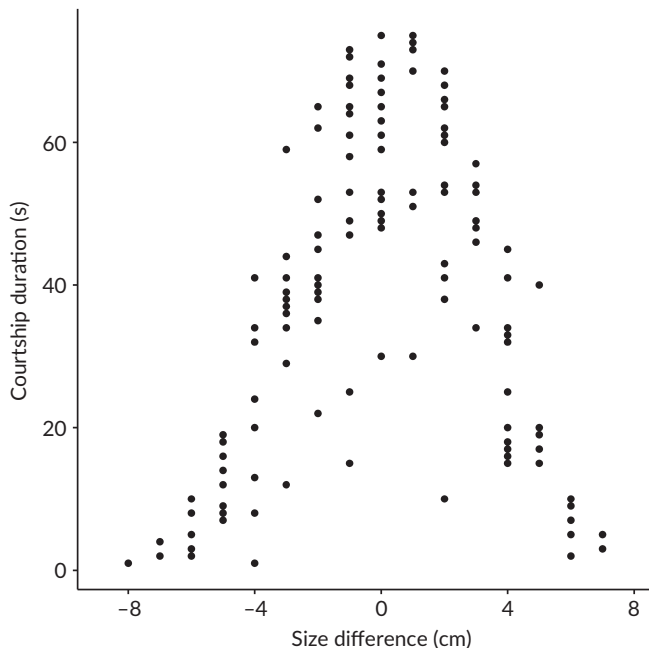


FIGURE 5 The relationship between duration of courting encounters and the difference in size between *Embiotoca jacksoni* pairs: minus values, female larger than male; positive values, male larger than female ($n = 150$)

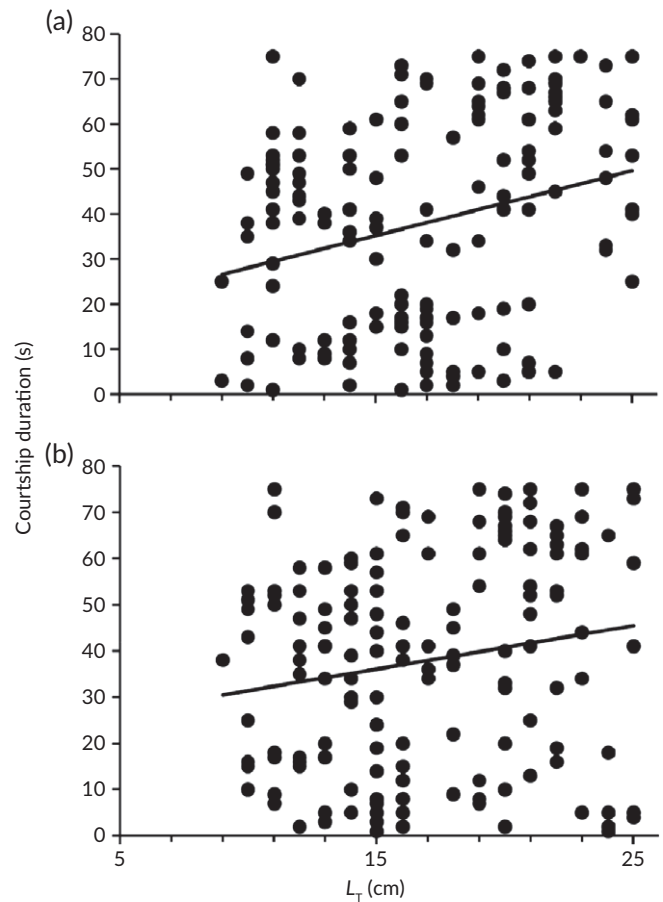


FIGURE 6 Relationship between duration of courting encounters and total length (LT) of (a) males and (b) females ($n = 150$ for both (a) and (b))

reduce their rate of foraging during the mating season, whereas males foraged at less than half the rate they did prior to the mating season. We interpret this finding as evidence that time spent courting is more valuable to males than females. That is consistent with optimal foraging theory (Schoener, 1971), which predicts that in mating systems in which males rely on courtship displays to attract mates and territorial aggression to exclude other males from using good mating sites, males should minimise time spent foraging in order to maximise reproductive success. Our results are also consistent with the prediction of optimal foraging theory that females should maintain a high rate of foraging during the mating season in order to ensure adequate energy and nutrients are available to develop offspring. Doing so may be especially important for female *E. jacksoni* and other livebearers, which must provide developing embryos with nutrients for several months prior to parturition. In *E. jacksoni* the energetic costs females incur from provisioning offspring during gestation must approximately equal energy intake foregone by males during the mating season because males and females grow at the same rate (Froeschke *et al.*, 2007).

The similarity between males and females in foraging rates prior to the mating season suggests that males are foraging maximisers (*sensu* Schoener, 1971) outside of the mating season. High rates of food intake during that period could benefit males in at least two

ways. First, it could help them build up energy reserves needed to carry them through the mating season when they feed less in order to have greater mating opportunities. These energy reserves are notably present as visceral fat, which reaches its maximum mass just prior to the mating season (M. Steele, unpubl. data). Second, high foraging rates outside of the mating season should result in high growth rates and there are several advantages to being larger. In the present study, we found that larger males tended to have higher courtship success (as estimated by courtship duration). Larger individuals also fare better in competitive interactions; e.g., over territories, which large male *E. jacksoni* sometimes establish (Hixon, 1981). Moreover, larger size in fishes generally results in lower mortality rates (Johnson *et al.*, 2014; Sogard, 1997). In this context, we expected that small individuals would benefit from maximising foraging effort, despite lost courting opportunities. Although that appeared to be the case in females, small males decreased foraging effort during the mating season, apparently trading foraging off for courting.

We found that large males reduced their foraging rates more than medium sized or small males during mating season. Larger individuals probably have higher energy reserves and thus are able to withstand reduced food intake better than smaller fish. Also, large individuals in this study were slightly more successful at courting (based on duration of courtship) and, in general, are more likely to defend mating territories successfully (Hixon, 1981). Also, they may have more incentive to forego foraging to spend more time courting and defending their mating territory. Small males reduced their foraging rate as much or more than medium sized males during the mating season. The size-assortative courting we documented may provide incentive for small males to trade off fast foraging and concomitant faster growth rates during the mating season for the possibility of siring offspring with small females. Additionally, small, young males may learn from early courting and benefit by being more successful at mating in subsequent mating seasons (Brown & Laland, 2003; Witte & Nöbel, 2006).

We had expected that small males and females (< 13 cm L_T) would be juveniles, but individuals of both sexes as small as 9 cm L_T courted and were courted during the mating season. These findings were unexpected because Froeschke *et al.* (2007) reported that maturity in *E. jacksoni* in the Southern California Bight is not reached until age one, at a minimum size of about 13 cm L_T . Maturity in that study, however, was diagnosed by the age of the youngest gestating female captured and gestation takes approximately 6–7 months (Froeschke *et al.*, 2007). We speculate that smallest individual was near parturition and had been much smaller when inseminated. Based on our observations of courtship in individuals as small as 9 cm L_T , combined with known growth rates (Froeschke *et al.*, 2007), we suggest that *E. jacksoni* at our study site mature and engage in courtship within 5–6 months of birth and inseminated females give birth about 6 months later, at 1 year of age and a size of at least 13 cm L_T . Precocious sexual maturity is common in the family Embiotocidae. For example, male *M. minimus* are born sexually mature and begin courting within weeks of birth (Hubbs, 1921).

Except for small males during the mating season, we found that small fish foraged at faster rates than larger fish. This pattern is

consistent with the prediction the small individuals should maximise their rate of foraging to accrue the benefits of larger size. Their faster rate of foraging, however, does not necessarily indicate higher mass-specific energy intake. Gape limitation restricts small embiotocids to foraging on small but abundant prey (e.g., gammarid amphipods: Ebeling & Laur, 1986; Ellison *et al.*, 1979; Schmitt & Holbrook, 1984) with lower calorific value per prey item than prey consumed by larger fish (e.g., decapods and polychaetes). Estimates of calorific value of common prey of *E. jacksoni* would be useful in understanding the consequences dietary shifts with body size. We expect that the decline in foraging rate with body size that we documented may be driven by larger fish specialising on larger, more energy-rich prey that smaller individuals cannot consume. Mass-specific growth rate (g g^{-1} initial mass), however, is fastest for small, young, *E. jacksoni* and declines with age and size (Froeschke *et al.*, 2007), suggesting there is a growth reward for rapid foraging by small individuals. Based on longer courtship times and the fact that long courtships appear more likely to result in mating, larger fish were more likely to mate than were smaller fish. Although the predictive power (r^2) of the relationship between size and courting time was not high, on average, the largest males we observed courted nearly twice as long as the smallest males and the largest females were courted about 1.5 times as long as the smallest females. This pattern implies that there is a reproductive advantage to larger size for both sexes, despite size-assortative courtship.

Courtship initiation by male *E. jacksoni* and duration of courtship were both size assortative, with males tending to initiate courtship with similar size females and courtship between similarly sized pairs lasting longest. We found no evidence that mate choice of larger individuals by males or females drives courtship success (Figure 5). This finding was unexpected because mate selection of the largest mates available by males and females is common in fishes (Côté & Hunte, 1989; Sargent *et al.*, 1986), presumably because reproductive fitness is often greatest for the largest individuals (Andersson, 1994; Clutton-Brock & Parker, 1992). Size-assortative courtship may occur in fish when courting large individuals is costly and unlikely to lead to mating (McKaye, 1986). For example, size-assortative courtship initiation and success in the small surfperches *C. aggregata* and *M. minimus* is thought to be the result of low mating success of small males with large females due to lack competitive dominance in *C. aggregata* (DeMartini, 1988) and due to the high energetic cost of mating in *M. minimus* (Warner & Harlan, 1982). The surfperch *Brachyistius frenatus* Gill 1862, however, does not show size-assortative courtship, courting females of all sizes in one study (Tootell & Steele, 2012) and females of equal or smaller sizes in another study (DeMartini, 1988). This variation among species of embiotocids suggests that different species experience different costs associated with courting. The present study demonstrates a trade-off for *E. jacksoni* between foraging and courting such that time spent courting comes at the cost of lost energetic gain via missed foraging opportunities. Live-bearing species may be particularly sensitive to these costs given that fecundity and survival of offspring are positively related to food availability (Okamoto *et al.*, 2012). Future measurements including time budgets

for courtship and foraging, as well as calorific value of prey are needed to quantify exact the energetic costs of reproductive trade-offs.

Overall, our results indicate that male and female *E. jacksoni* face different trade-offs between foraging and mating. Males forage less during the mating season presumably to dedicate time to courting females, whereas females do not alter their foraging behaviour much. These differences likely stem from the mating system, in which males compete for mating opportunities over a period of 1 month or more and females probably spend little time mating. Females then carry developing offspring for several months and consistently forage at high rates allowing for provision of maternal nutrition *in utero*. Our study suggests that a sound understanding of mating systems may enable more accurate predictions of how foraging-mating trade-offs are made in other species.

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Contributions

D.R.S contributed to concept, data generation, data analysis, manuscript preparation.

M.A.S contributed to data analysis, manuscript preparation.

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