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Animal behaviour

Does male reproductive effort increase with age? Courtship in fiddler crabs

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Theory suggests that reproductive effort generally increases with age, but life-history models indicate that other outcomes are possible. Empirical data are needed to quantify variation in actual age-dependence. Data are readily attainable for females (e.g. clutch per egg size), but not for males (e.g. courtship effort). To quantify male effort one must: (i) experimentally control for potential age-dependent changes in female presence; and, crucially, (ii) distinguish between the likelihood of courtship being initiated, the display rate, and the total time invested in courting before stopping ('courtship persistence'). We provide a simple experimental protocol, suitable for many taxa, to illustrate how to obtain this information. We studied courtship waving by male fiddler crabs, *Uca annulipes*. Given indeterminate growth, body size is correlated with age. Larger males were more likely to wave at females and waved more persistently. They did not, however, have a higher courtship rate (waves per second). A known female preference for males with higher display rates explains why, once waving is initiated, all males display at the same rate.

1. Introduction

Life-history theory generally predicts an increase in reproductive effort with age as residual reproductive value declines [1]. This is sometimes misinterpreted to mean that reproductive effort must increase with age [2,3]. However, optimization life-history models show that other outcomes are possible ([4, p. 259]). Additionally, game theory models of sexual selection note that variation in individual quality (genetic or environmental) can affect survivorship and investment patterns [5]. Quality-dependent ontogenetic shifts in reproductive effort and survival determine the observed relationship between age and reproductive effort [3,5].

Many studies report that sexual ornamentation or courtship display intensity increases with age [6], but this is not always the case. For example, in the cricket *Teleogryllus commodus*, males on a high-quality diet called more when young and, consequently, died sooner than those on a low-quality diet who called less when young [7]. More generally, if there are age-dependent costs and/or benefits of courtship, courtship effort could increase, decrease or remain unchanged with age [5,6].

Estimating female reproductive effort (i.e. fecundity) is often more straightforward than estimating that of males (e.g. mating effort). Unfortunately, if males only display in response to female presence, then there are practical problems in determining how reproductive effort changes with age. Courtship rate alone provides an incomplete picture. It is also necessary to quantify a male's propensity to initiate and then persist in courtship [8]. This is often achievable only by experimentally controlling for female presence. To date, most studies of age-dependent courtship are observational, quantifying courtship rates or total courtship time without controlling for female presence [3,6].

We experimentally tested for age-dependent courtship in the fiddler crab *Uca annulipes*. Crabs have indeterminate growth [9], so size is a reasonable proxy for age [10]. Males wave their enlarged claw to court females [9]. Waving is energetically costly [11] and related to body condition [12]. Observational studies have investigated the relationship between male size and sexual display in some fiddler species [13,14], but age-dependent courtship has not been explicitly addressed. We experimentally standardized female presence to determine how male age/size is related to: (i) the likelihood of initiating courtship; (ii) courtship rate; (iii) courtship persistence; and (iv) the effect of female size on male courtship.

2. Material and methods

We studied *U. annulipes* in Chukwani mangroves, Zanzibar (September–October 2010). By remaining stationary, we made observations from less than 2 m away without disturbing crabs [12,15–17].

(a) Are males of all ages equally likely to wave at females?

We selected focal males with brachychelous claws (size range: 11.0–31.7 mm claw length, CL) before the daily onset of waving to ensure we had no prior information about their courtship propensity. We then captured females (6.8–14.0 mm carapace width, CW) to use as stimuli. In each trial, we placed a female inside a 5 cm diameter, transparent plastic collar pushed into the sediment 10 cm from the male's burrow. These females stimulated focal males to wave. When the focal male re-emerged from his burrow, we noted whether he waved at the female. To be classified as waving, he had to give greater than or equal to five waves within 5 min. This accommodated the low level of non-directed 'background' waving seen in *U. annulipes*. We then measured male CL and female CW (± 0.1 mm) with callipers ($n = 43$ unique pairs).

(b) Does male courtship display vary with age?

We followed the earlier-mentioned protocol except that, because we were interested in courtship rate and persistence, we selected only males already observed courting that day. We presented each focal male with a stimulus female (male CL: 11.8–30.5 mm; female CW: 6.6–14.3 mm). When he commenced waving, we counted how many waves were produced, and the bout duration (first to last wave). We defined the last wave when more than 30 s elapsed without waving ($n = 101$ unique pairs).

In both experiments, variation in the number of male neighbours or passing mate-searching females could introduce statistical noise. Other sources of uncontrolled variation include differences in stimulus female activity level, and her average position within the plastic enclosure. Consequently, our estimates of male-size effects are conservative.

(c) Statistical analyses

Courtship rate was calculated as total waves per bout duration. Courtship persistence was defined by either the duration of the courtship bout or the total number of waves. We ran a binary logistic regression to test whether males of all sizes/ages were equally likely to initiate courtship. To determine whether male age and female size affected courtship rate or persistence, we ran general linear models with bout duration, wave count or wave rate (all log-transformed to fit parametric

assumptions) as dependent variables and male and female size as predictors. We included 'day in tidal cycle' and 'time relative to low tide' in models as they can influence waving [15]. To analyse wave rate, we excluded 12 males that gave too few waves (0 or 1) to calculate wave rate. All data have been deposited in Dryad (<http://dx.doi.org/10.5061/dryad.44r25>).

3. Results

(a) Are males of all ages equally likely to wave at females?

Larger/older males more often initiated waving (Wald $\chi^2_1 = 10.687$, $p = 0.001$; odds ratio: 1.49; 95% CI: 1.17–1.88). The mean claw size was 21.4 ± 4.2 mm ($n = 20$) for waving males, and 15.8 ± 3.8 mm ($n = 23$) for non-wavers. Female size did not affect whether a male waved (Wald $\chi^2_1 = 1.723$, $p = 0.189$; odds ratio: 1.31; 95% CI: 0.88–1.97).

(b) Does male courtship display vary with age?

Larger/older males were significantly more persistent when courting, with longer courtship bouts and more waves produced (table 1). There was, however, no significant effect of male size/age on wave rate. Female size and time in cycle or relative to low tide had no detectable effect on courtship (table 1).

4. Discussion

In our study, larger/older male *U. annulipes* were significantly more likely to wave at females, waved for longer and gave more waves than younger males. They did not, however, have a higher wave rate. Life-history models often predict that older individuals will invest more effort into reproduction [1], but alternative relationships are possible [4]. This is partly due to age/size-dependent changes in mortality, fecundity and trade-offs that affect current and residual reproductive value. In fiddler crabs, mortality rate probably declines with size/age because predators, especially shorebirds, are gape-limited [16]. Male fecundity increases with size as larger males can mate with larger, more fecund females (large females cannot enter small males' burrows to mate). Additionally, the costs of courtship might be lower for older males. Waving is energetically costly [11], reducing growth, while females show a directional but asymptotic preference for larger males. Consequently, younger males might benefit by reducing their reproductive effort. Furthermore, the benefits of courtship are probably greater for older males, because females prefer males with larger claws increasing the likelihood that waving leads to mating [18]. Observational studies of other fiddler species also suggest that courtship effort increases with size (e.g. in *Uca pugilator*, larger males feed less and wave more often) [13]. One 'proximate' explanation for our finding is that larger males might more strongly stimulate neighbours to wave, which then stimulates the focal male to wave more himself. It is also possible that larger males might have greater visual acuity, which would increase their ability to detect and assess females and respond accordingly. There is, however, currently no evidence for these two proposed mechanisms.

Table 1. General linear models testing how male and female size and time relative to low tide affect male courtship. Asterisks denote significant at $p < 0.05$.

response variable	source	B	s.e.	SS	d.f.	F	p
courtship bout duration (s)	male size	0.055	0.021	5.516	1	7.046	0.009*
	female size	0.066	0.047	1.544	1	1.985	0.162
	male × female size	−0.014	0.008	2.152	1	2.749	0.101
	time relative to low tide	0.001	0.002	0.695	1	0.888	0.348
	day in cycle	0.040	0.089	0.157	1	0.201	0.655
	error			74.370	95		
total number of waves given	male size	0.041	0.017	3.057	1	5.419	0.022*
	female size	0.067	0.040	1.568	1	2.779	0.099
	male × female size	−0.011	0.007	1.394	1	2.471	0.119
	time relative to low tide	0.001	0.001	0.165	1	0.292	0.590
	day in cycle	0.017	0.076	0.030	1	0.053	0.818
	error			53.597	95		
wave rate (waves per second)	male size	0.001	0.004	0.002	1	0.063	0.802
	female size	0.016	0.010	0.062	1	2.380	0.127
	male × female size	−0.001	0.002	0.007	1	0.271	0.604
	time relative to low tide	<0.001	<0.001	0.001	1	0.057	0.813
	day in cycle	0.010	0.018	0.008	1	0.320	0.573
	error			2.224	82		

Our study highlights the danger of the standard approach of using courtship rate to infer male reproductive effort. In *U. annulipes*, older males did not wave at a higher rate than younger males. Yet, it is unlikely that female mating decisions are based on courtship bout duration. The natural interval over which females sample a male is generally far shorter than the bouts we recorded [19] (bouts were extended because the female remained until the male ceased courtship). Studies using robotic crabs show that females prefer higher wave rates [19]. Consequently, because males compete with their neighbours, a male gains little by waving at a lower rate than his immediate competitors. Once courtship is initiated, smaller males should therefore court at the same rate as larger males until they can no longer persist. So the question is then—how often and for how long do males court?

Our study design allowed us to detect the lower reproductive effort of smaller/younger males, because we documented the likelihood of initiating courtship and then their courtship persistence. Ideally, an index of male reproductive effort should measure 'attendance' at mating rather than foraging sites (e.g. lek attendance in birds). In the case of fiddler crabs, however, males both court and feed from their burrows. The likelihood of waving when a female is present is therefore the best measure of a male's decision to switch from feeding to investing in mating attempts.

The need to distinguish between courtship initiation, rate and duration is exemplified by a study of another *U. annulipes* population that reported a positive relationship between male size and wave rate [12]. This observational study failed to account for female encounter rate or variation in the initiation and duration of waving, making it impossible to determine whether net investment in waving was actually greater for older males. It is, of course, possible that conspecific populations differ in age-dependent sexual advertisement [20].

In conclusion, we suggest that to quantify age-dependent changes in mating effort we need to control experimentally for female presence and look at male responses to mating opportunities. Unlike morphological sexual traits, male displays (aside from long-range attraction) often depend on female presence. We recommend that researchers distinguish between the likelihood of courtship initiation, courtship rate and persistence of courtship. These combined measures provide a fuller picture of male investment decisions. Simple experiments such as ours, perhaps using female models, could readily be used in other taxa (e.g. lekking birds or mammals, and insects with close-range courtship).

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