Patricia R.Y. Backwell · Michael D. Jennions
John H. Christy · Ursula Schober

Pillar building in the fiddler crab *Uca beebei*: evidence for a condition-dependent ornament

Abstract In the fiddler crab (*Uca beebei*) males build a small mud pillar next to their burrow which increases their attractiveness to females. Three hypotheses were tested to explain inter-male variation in pillar-building. (1) The benefits of pillar-building are density dependent. The experimental addition of vertical structures did not support this hypothesis as there was no change in the level of pillar-building. (2) There are two classes of males (pillar-builders and non-pillar-builders). This could either be due to an alternative mating strategy, or because pillar building is age or size-dependent. There was also no support for this hypothesis. (3) Pillar-building is an honest signal of male quality dependent on body condition. A food supplementation experiment was performed. Addition of food affected several aspects of male behaviour and resulted in a two fold increase in the number of pillars built between control and food treatments ($P < 0.001$). However, the percentage of males building pillars did not increase significantly. Pillar building in this species has been attributed to sensory exploitation. Our results indicate that a trait which may well have evolved through sensory exploitation also appears to be condition-dependent. We emphasise that showing that an ornament or behaviour is condition-dependent does not necessarily mean that it evolved through "good gene" processes. However, in terms of its current selective value, pillar building may be maintained through female choice because it acts as a signal of male condition.

P.R.Y. Backwell (✉)[1] · J.H. Christy · U. Schober
Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Republic of Panama

M.D. Jennions
Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, UK

Present address:
[1] Department of Zoology, University of the Witwatersrand, Private Bag 3, WITS 2050, Johannesburg, South Africa

Introduction

There is now good empirical evidence from a wide variety of mating systems (reviewed in Møller 1994) that female mate choice can lead to selection for extravagant or bizarre male traits ("ornaments"). Historically, the two most important models for the evolution of female choice due to indirect "genetic" gains are the "Fisherian" and "handicap" models. In both cases the female preference and male ornament co-evolve (Pomiankowski and Sheridan 1994). Fisherian models predict that female preferences for arbitrary male phenotypes lead to increased elaboration of both preference and trait through positive feedback (Lande 1981; Kirkpatrick 1982: Pomiankowski et al. 1991). Handicap models predict that preference and ornament co-evolve, but that each male balances the mating benefits gained from the ornament against his ability to withstand the cost of increasing the magnitude of the ornament (Zahavi 1977; Grafen 1990a, b; Iwasa et al. 1991). If more viable males pay a smaller cost for an increase in ornamentation, it will generally act as an honest signal of male quality.

Work investigating the costs of ornamentation provides important information on the selection pressures limiting their expression, and how these costs vary between males (Sutherland and De Jong 1991; Höglund et al. 1992). In most cases, however, knowledge about the current relationship between costs and male quality does not allow definitive conclusions about which of the two "genetic" models is more applicable. The two processes may have indistinguishable outcomes, and it has been difficult to formulate unique predictions that discriminate between the models (Balmford

and Read 1991; but see Balmford et al. 1993; Jennions 1993).

More recently, a third process has been proposed to account for the evolution of ornaments (Ryan 1990). Males may exploit pre-existing female sensory biases that arise as by-products of direct selection on females for other activities (Ryan 1990; Enquist and Arak 1993). Two forms of evidence have been presented to support the "sensory exploitation" hypothesis. First, a match may be shown between a male courtship trait and a female preference or behavioural bias that occurs in a non-courtship context, such as foraging or predator evasion. Evidence of this sort has been collected for fiddler crabs (Christy 1988b), water mites (Proctor 1991) and fruit flies (Bennet-Clark and Ewing 1967). Second, phylogenetic information may be used. If a female preference evolved prior to the ornament, the two need not have co-evolved. The male trait may simply have evolved to exploit the pre-existing female preference. Phylogenetic analyses suggest the possible evolution of preference prior to ornament in two separate lineages (frogs: Ryan and Rand 1993; but see Pomiankowski 1994; water mites: Proctor 1992). A well-known example from swordtail fish (Basolo 1990) has recently been questioned in the light of a molecular phylogeny (Meyer et al. 1994). Possible mechanisms generating sensory biases have been proposed by Ryan and Keddy-Hector (1992), Enquist and Arak (1993) and Weary et al. (1993).

When females mate preferentially with males that have larger ornaments, it would appear beneficial for all males to invest equally. The three models for the evolution of female choice provide different explanations for variation in male ornamentation. According to handicap models, variation in ornamentation is the inevitable outcome of variance in male quality (Grafen 1990b). In contrast, Fisherian models assume that ornament expression is largely genetically fixed (Evans 1991) and that variation in ornamentation predominantly reflects this genetic basis. If an ornament has evolved through sensory exploitation then, as with a Fisherian trait, it need not reflect male quality and, in principle, all males should invest equally. Unfortunately, because the endpoint of all three processes is a costly ornament, ornamentation may co-vary with male quality regardless of the historical origins of the trait (Balmford and Read 1991).

Another explanation for variation in ornamentation is that its benefits vary independently of male quality or genotype. For example, if frequency or density-dependent factors limit the ability of females to assess males, this may explain why some males do not exhibit the preferred trait. Similarly, local environmental differences may cause intra-population variation in phenotypically plastic ornaments, as does variation in natural selection pressures between populations or species (Balmford et al. 1993; Marchetti 1993).

We investigated male ornamentation in the tropical fiddler crab *Uca beebei*. Previous studies of mating success show that females are more likely to mate with males that build a mud pillar at the burrow entrance (Christy 1988b). This mating bias has been interpreted as the outcome of sensory exploitation of females by males (Christy 1988b; Christy and Salmon 1991). Experiments show that females enter burrows with pillars more often than those without pillars when threatened by an artificial predator (Christy 1988b). However, females sampling males prior to mating are no more likely to stay and mate in a burrow with a pillar than in one without (J.H. Christy, unpublished work). This suggests that pillars serves only to attract females to burrows, and that increased attractiveness exploits female anti-predator behaviour.

The study animal and three hypotheses for variation in pillar building

Uca beebei is a small fiddler crab (carapace width about 1 cm) that occurs on estuarine mudflats on the Pacific coast of Central America and northern South America. Males and females defend burrows in the inter tidal zone and are active during the low tide period. Males court females that wander on the surface with claw-waving and other behavioural displays (Crane 1975; Christy 1988a). In addition to behavioural displays, males sometimes build a 2-cm-high mud pillar at their burrow entrance which increases a male's attractiveness (Christy 1988b). Earlier work showed that pillars do not convey information on burrow quality. The mating preference for males with pillars appears to be unrelated to "material" benefits (Christy 1988b). There is also no evidence that pillars function in male-male competition (Christy 1988a). Pillars are built anew each low-tide period, because they are destroyed by the incoming tide.

Despite the mating benefit gained by possessing a pillar, daily less than half the males present build pillars (Christy 1988a). Why do not all males build pillars every day? We tested three hypotheses that might account for variation in pillar-building.

1. Environmental variation in benefits: pillars are thought to attract females because they exploit the enhanced vertical resolution of crab eyes (Zeil et al. 1986; Christy 1988b). An increased density of vertical structures, such as pillars, may reduce the conspicuousness of individual pillars leading to diminished benefits in terms of attractiveness. Independent of absolute density, the proximity of vertical structures may act as a cue males can use to estimate the density of vertical structures.

2. Two classes of males: the population may be polymorphic with two classes of males: pillar-builders

and non-pillar-builders. Past research on *Uca beebei* has not involved individually identifiable males observable over extended periods. Another possibility, unrelated to the existence of two genuine classes, is that the tendency for males to build pillars varies through time. For example, there may be a reproductive cycle (unsynchronized between males) involving pillar-building and non-pillar-building phases.

3. Increased costs: males may vary in their ability to sustain costs associated with pillar-building. Males with pillars spend less time feeding than males that do not build pillars (Christy 1988b), suggesting that pillar-builders are better fed and can afford to forage less. Pillar-building itself seems energetically inexpensive. On average, it takes less than 10 min to construct a pillar. However, there may be further costs attached to possession of a pillar. For example, owners may spend increased time and/or energy defending the burrow from non-receptive females and burrowless males, or stand a greater risk of predation if pillars make burrows more conspicuous.

Methods

Study site

Field work was conducted in the Republic of Panama during December 1991–April 1992 by P.R.Y.B. and a field assistant. The study was conducted on an inter-tidal mud flat (Rodman flat) on the west bank of the Panama Canal, approximately 1 km upstream from the Bridge of the Americas. All experiments and observations were carried out in a 200-m² area of mud flat. The amplitudes of the semi-diurnal tides ranged from 2 to 6 m during the study. Crabs emerged from their burrows and were active on the surface for about 4.5 h each day during the diurnal low tide. Crabs are not active on the surface before sunrise or after sunset (Christy 1988a).

Changing benefits: altering the density and proximity of vertical structures

We painted wooden dowel-rod pegs (diameter = 1.5 cm, height = 2.5 cm) black, and supported them with a 4 cm long metal pin. These were thrust into the sediment so that 2.0 cm of the peg was above the mud surface (vertical pegs). To control for any disturbance caused by the insertion of pegs, 0.5-cm-high pegs were used as controls (control pegs). These were thrust into the sediment until flush with the surface.

We delimited six 1-m² plots with twine supported 10 cm above the sediment surface. All plots fell within the area of maximum crab activity. Approximately 2 h before low tide, and always prior to pillar-building, we added pegs to plots. In the first experiment (14 days during December 1991–January 1992), we randomly placed 20 vertical pegs in each of three plots and control pegs in the other three plots. The type of peg used on a plot was switched each day. Each plot thus acted as its own control. In the second experiment (14 days during January–February 1992), we placed a peg approximately 1 cm away from each open burrow entrance. Each day, vertical pegs were added to three plots and control pegs to the other plots. The peg type used in a plot was switched each day. After peg addition, plots were left undisturbed for 2–3 h. At 1 h after low tide we counted the number of pillars built per plot, and pegs were then removed. In the second experiment, we also counted the number

of males present per plot (three counts of male numbers were made at 10-min intervals and the largest value recorded).

Energetic costs: the addition of food

We constructed four 1-m² cages on the mudflat. Cages were made from 30-cm-high, moulded plastic netting with 0.4 cm diameter pores (4 pores/cm²), inserted 15 cm into the sediment. To prevent crabs escaping, PVC tubing (diameter = 2 cm) was slit and threaded onto the top of the walls and connected by PVC elbows at the corners. An observer was always present during periods of male activity, and only one male escapee was seen. It is thus highly unlikely that observed changes in male activity were due to males leaving the cages. Artificial burrows (one per individual) were made using a hollow metal tube (diameter = 1.5 cm). Males with and without pillars were randomly selected, captured, individually marked and introduced onto plots. We marked males by gluing a small coloured plastic tag onto the dorsal carapace. Initially 30 marked males ($n=15$ with pillars) were introduced into each plot, seven males ($n=4$ with pillars) were added on day 18, and a further 10 males ($n=4$ with pillars) were added on day 29. Females were added to the plots throughout the study to stimulate male courtship behaviour ($n=20$ females per plot). We added food to two plots daily throughout the study. Food consisted of 5 g of Tetramin tropical fish flakes diluted in 0.5 l of sea water. The same volume of pure sea water was added to the control plots.

We made daily observations from 2 h before to 2 h after low tide for 53 consecutive days during February–April 1992, excluding days when low tide fell at sunrise or sunset. Observations were made from a 6 m high stepladder, using 8 × 30 binoculars. Each day we noted the following: the identity of all males present on the surface; the identity of pillar-building males; the time of pillar construction and the total number of pillars built. Analysis on an hourly basis did not add explanatory power, we therefore present results based on the daily data. Males that moult are no longer identifiable because identification tags are lost. Some data are thus relative measurements of male presence used for comparisons between different classes of males. "Days seen" refers to the number of days males were present on the surface. "Males resighted" refers to males that were seen at least once on the surface after the start of the experiment. All males were in the plots throughout the study, but varied in their tendency to appear above ground.

Statistical analyses

Most data were not normally distributed and could not be transformed. We therefore used standard non-parametric tests (Siegel and Castellan 1988). Summary statistics are presented as mean ± SD. In the enclosed plots we *operationally* defined two classes of males: those that built pillars (P-males) and those that did not build pillars (NP-males).

For the vertical structure-addition experiments, daily data from each plot were combined and presented in terms of "plot-days". This analysis assumes statistical independence between days for each plot, because treatments were changed each day. However, repeated measures from a plot might be regarded as "pseudoreplication". We therefore also calculated means for vertical and control pegs for each plot ($n=7$ days each). This yielded two data points per variable for each plots which we then compared using Wilcoxon tests.

For the feeding experiment, data from the two plots for each treatment (control and food-addition) were pooled to increase sample sizes and allow meaningful comparative testing. We first checked for significant differences between plots within each treatment. There were no significant differences within treatment type for the following variables: (1) number of males building pillars, (2) percent pillar builders (of males resighted), (3) pillars/day/male (P-males), (4) pillars/male (P-males), (5) days/male (P-males) and (6) days/male (NP-males) (Mann-Whitney U-tests, two tailed, all

$P > 0.05$). The percentage of males resighted differed between control plots, but not between food plots. However, given that 14 comparisons were made this is probably attributable to a type I error (1/14 = 0.07). The only variable which differed between plots was the absolute number of males present per day. However, this is not a key variable for our analyses, which deals primarily with variation in the level of pillar-building. In addition, food and control cages were positioned so that they were paired along the gentle gradient of male density seen across the mudflat which probably accounts for the observed difference between plots.

For comparisons between treatments which involved repeated measures from the same treatment (e.g., pillars/day) non-parametric runs tests were first performed to ensure that sample days were statistically independent. The time period between samples was increased until statistical independence was achieved. Comparisons between treatments were performed using Wilcoxon matched-pairs tests, because of temporal variation in male activity associated with the lunar tidal cycle. The treatment with the smallest number of independent days therefore determined sample sizes for two-sample comparisons. However, summary statistics are based on the largest sample of statistically independent days. In several cases clear predictions were made as to the direction of response to a manipulation, and one-tailed tests were used. All other tests are two-tailed. The alpha level of significance was set at $P=0.05$.

Results

Density-dependent benefits

The number of pillars built per day in plots when vertical pegs were added did not differ from that when control pegs were added (pillars: $\bar{x}\pm SD=5.98\pm2.96$; control: $\bar{x}\pm SD=5.86\pm3.16$, $n=42$ plot-days; Mann-Whitney U-test, $Z=0.25$, $P=0.81$). There were also no significant differences in the number of displaying males per day ($Z=0.17$, $P=0.86$), the number of pillars built per day ($Z=0.33$, $P=0.74$) and the percentage of the males present that built pillars each day ($Z=0.79$, $P=0.43$) when vertical pegs as opposed to control pegs were placed near burrow entrances.

To be more conservative, we re-analysed the results using the mean for each plot for control and vertical pegs. When the density of vertical structures was increased, there was no change in the number of pillars built per day (Wilcoxon matched-pairs test, $Z = 0$, $P = 1.00$). When vertical pegs were placed next to each burrow, there was also no significant change in any of the measured variables (Table 1). In conclusion, neither the density nor proximity of vertical structures affected pillar-building or male presence.

Energetic costs: effects of food addition

The results of this experiment are summarised in Table 2. The number of pillars built with food supplementation was more than double that in the control ($\chi^2=75.06$, $df=1$, $P<0.001$). There were also more pillars each day and a greater percentage of males on the surface building pillars each day with food supple-

Table 1 The number of displaying males, pillars built and percentage of males building pillars in plots when either pillar pegs or control pegs were placed near burrow entrances. Means ($\pm SD$) are shown. Results of two sample comparisons between means for each of 6 plots (Mann-Whitney U-tests) are also shown

	Number of males	Number of pillars	Percent pillar-builders
Pillar	23.6 (±5.7)	4.5 (±1.8)	17.3 (±4.7)
Control	22.9 (±6.1)	4.2 (±1.8)	19.8 (±4.2)
Test statistic	$Z = 0.08$	$Z = 0.40$	$Z = 0.72$
P	0.94	0.35 [a]	0.24 [a]

[a] one tailed

mentation. Hence food had a positive effect on levels of pillar-building throughout the study, and did not simply cause an initial burst of activity. There was a non-significant increase in the percentage of males that built pillars when food was added ($P=0.09$). Thus the increased number of pillars built when food was added was due to higher levels of pillar-building by a subset of the population. We therefore examined the behaviour of pillar-building males more closely (Table 3). As expected, individual P-males built more pillars in the food supplementation treatment compared to the control. There was, however, no significant difference in the mean number of pillars per day for P-male between food supplementation and control treatments, although the duration of the pillar-building cycle decreased in the presence of extra food (Table 3). Over all, the number of pillars built per male was greater with food supplementation (Mann-Whitney, one-tailed, $Z=1.89$, $P=0.03$).

Given that the total number of pillars built increased significantly with supplementary food, it is anomalous that neither the percentage of P-males, the number of days present per P-male (Table 2), or pillars/day for P-males (Table 3) increased significantly. The significant increase in pillars built may be attributable to the interaction between the non-significant increases in the number of males building pillars (38 males versus 28 males) and in the number of days present per P-male (19.2 days versus 16.3 days).

Food supplementation significantly increased the number of males present per day. There was, however, no difference in the absolute number of male resighted on the surface (73% versus 63%). Food addition also had no effect on the mean number of days that each male was active on the surface. This result held when the data was analysed separately for P-males and NP-males (Table 2).

Temporal variation in male behaviour

Males tended to build pillars in bouts lasting several days. The distributions of the number of consecutive days between days on which a pillar was built were

Table 2 Male activity in enclosed plots with and without addition of food over 53 days (n=94 males per treatment). Means (±SD) are shown. Only P-males built pillars during the caged study. *Males resighted* refers to all males seen above ground. Results of two-sample comparisons are shown. Tests comparing amount of pillar-building are one-tailed, the rest are two-tailed

	Food	Control	Test statistic	P
Total number of pillars built	376	173	$\chi^2=75.06$	<0.01
Percentage of males resighted	73.4% (n=69)	62.7% (n=59)	Fisher exact	0.16
Percent P-males (of males resighted)	55% (n=38)	48% (n=28)	Fisher exact	0.25
Percent P-male	40%	30%	Fisher exact	0.09
Males/day	31.5 (±12.1)[e]	20.9 (±7.6)[c]	Z= 2.27	0.02[a]
Pillars/day	7.2 (±6.9)[c]	3.3 (±3.2)[d]	Z= 3.02	<0.01
Percent pillar builders/day	18.9 (±16.9)[f]	14.8 (±14.4)[f]	Z= 2.00	0.02[a]
Days seen/male	13.2 (±10.7)	10.3 (±8.9)	Z= 1.37	0.17[b]
Days seen/P-male	19.2 (±10.2)	16.3 (±8.7)	Z= 0.97	0.33[b]
Days seen/NP-male	5.7 (±5.2)	4.9 (±4.5)	Z= 0.46	0.65[b]
Pillars/male	2.2 (±3.8)	1.1 (±2.5)	Z= 1.89	0.03[b]
Pillars/male (for males resighted)	3.0 (±5.5)	1.8 (±3.9)	Z= 1.73	0.04[b]

[a] Wilcoxon signed-rank tests with comparison based on every 2nd or 3rd day as this was the largest sample size for which days were statistically independent in both samples (males/day: n=18 days; pillars/day: n=27 days; percent pillar builders/day: n=18 days)

[b] Mann-Whitney U-tests

[c] Based on data from every 2nd day to ensure statistical independence (n=27 days; runs tests: food: Z=1.39, P=0.16; control: Z=−0.90, P=0.37)

[d] Based on all 53 days, as runs tests showed that they were statistically independent (runs test: Z=1.18, P=0.24)

[e] Based on every 3rd day as these were statistically independent (n=18 days; runs test: Z=0.53, P=0.60)

[f] Based on every 3rd day as these were statistically independent (n=18 days; runs test: food: Z=1.42, P=0.16; control: Z=1.18, P=0.24)

Table 3 Behaviour of pillar-building males (P-males) in enclosed plots with (n=38 males) and without (n=28 males) the addition of food. Mean (±SD) are shown. Results of two sample comparisons (Mann-Whitney U-test) are also shown

	Pillars/male	Pillars/day	Duration of pillar-building cycle (days)
Food	5.5 (±4.1)	0.28 (±0.15)	7.1 (±2.9)
Control	3.9 (±3.3)	0.25 (±0.17)	9.3 (±4.5)
Test statistic	Z = 1.73	Z = 1.20	Z = 2.02
P	0.04 [a]	0.12 [a]	0.04

[a] One-tailed

compared to normal and even distributions. In both food and control treatments the distributions were highly skewed (χ^2 goodness-of-fit test to even distribution: control: $\chi^2=316.32$, $df=14$, $P<0.005$; food: $\chi^2=2176.98$, $df=18$, $P<0.005$: to normal distribution: control: $\chi^2=424.77$, $df=5$, $P<0.005$; food: $\chi^2=582.9$, $df=7$, $P<0.005$). With the food treatment, 81% of pillars were built on days consecutive to one where the male had built a pillar. In the control, the corresponding figure was 70%. The distributions differed significantly between treatments (Kolomogorov-Smirnov, $D=0.70$, $P<0.01$). This difference was due to a change in the inter-bout interval and not in the length of the actual bouts of pillar building (see below).

The tidal-lunar cycle has well-known effects on daily levels of activity in *Uca* species (Crane 1975). Additional variation in activity is, however, also apparent. In *Uca beebei* males undergo longer-term cycles of reproductive activity. Males pass through a period of irregular waving and tend to remain in their burrows. Gradually the amount of time spent on the surface increases until a male spends most of the low tide period displaying vigorously. He then builds pillars for a number of consecutive days, occasionally skipping a day, after which his activity level again decreases. These cycles of individual male activity do not appear to be synchronised between males, and were highly variable in duration (Coefficient of variation: 41% and 48% in food and control plots respectively). "Building-bout" length was calculated as the number of days between the start and termination of pillar-building, with a maximum of 1 day without pillar-building being allowed before a new bout was recognised. A male's pillar-building cycle was measured as the number of days between the start of successive building bouts. Interestingly, food addition significantly decreased the duration of pillar-

Table 4 Spearman rank correlation coefficients (r_s) between days present and number of pillars built, and pillars per day for pillar-building males in the food addition ($n=38$ males) and control plots ($n=28$ males)

	Food addition	Control
Number of pillars	0.46 *	0.76 **
Pillars/day	−0.14	0.21

* $P<0.05$, ** $P<0.01$

building cycles (Mann-Whitney, $Z=2.02$, $P=0.04$), but not the duration of building bouts (Mann-Whitney, $Z=0.93$, $P=0.35$) (Table 3).

Data from the 28 P-males in the control plots and the 38 P-males in the food plots were analysed with respect to the number of days present and the number of pillars built (Table 4). There was a strong positive correlation between days present and number of pillars built in both treatments. There was, however, no significant correlation between the number of days present and the number of pillars built per day. Considering all males (NP and P-males) that were active, there was also a significant correlation between days present and the number of pillars built per day (food: $r_s=0.48$, $P<0.01$, $n=69$; control: $r_s=0.64$, $P<0.01$, $n=59$).

Classes of males

When we captured the 188 males for the feeding experiment, we first noted whether or not they were from a burrow with a pillar. Of the 62 males classified as NP-males based on their behaviour during the experiment, 31 (50%) had previously built a pillar. This leaves the remaining 31 males as potential candidates for a genuine class of non-pillar-builders. To test the likelihood that they really were non-pillar-builders, we compared the distribution of days before each P-male first built a pillar with the distribution of days present for the 31 NP-males that did not possess pillars when first captured. There was no significant difference between the distributions (Kolomogorov-Smirnov, two-sample test, $D=1.36$, $P=0.30$). This suggests that the 31 potentially genuine non-pillar-builders were observed for insufficient time to see them build pillars.

The number of days that P-males and NP-males were seen on the surface differed significantly (control: P-males: $\bar{x}\pm SD=16.43\pm8.85$; $n=28$; NP-males: $\bar{x}\pm SD=4.93\pm4.49$, $n=31$; $Z=5.39$, $P<0.01$; food: P-males: $\bar{x}\pm SD=16.95\pm11.13$, $n=38$; NP-males: $\bar{x}\pm SD=7.68\pm7.77$, $n=31$; $Z=3.96$, $P<0.001$, both Mann-Whitney tests). Can this difference in daily presence explain the existence of NP-males? To assess the importance of this variable we examined its effect on pillar-building. The mean number of pillars/day built by P-males who were present for fewer days ($\leqslant 10$ days) did not differ from that of males present for more days

($\leqslant 10$ days P-males: $\bar{x}\pm SD=0.29\pm0.22$ pillars/day, $n=10$; $\geqslant 10$ day P-males: $\bar{x}\pm SD=0.22\pm0.14$ pillars/day, $n=18$; Mann-Whitney U-test, $P=0.36$). Hence days present does not have a strong effect on the rate of pillar building. However, the overall likelihood of building at least one pillar does increase with days present (Table 4).

Discussion

The results of our study of individually marked males showed that some males did not build pillars. Perhaps more importantly, even males that built pillars did not do so every day that they were active on the surface. Three hypotheses were tested to account for variation in pillar-building activity.

First, the addition of vertical pegs indicated that pillar-building is influenced neither by the density nor the proximity of vertical structures. Pillars are the most common vertical structures on the mudflat. Our results thus provide no support for the hypothesis that the density of vertical structure and possible variation in the benefits of possessing a pillar account for variation in pillar-building. These results support a separate field study in which the number of pillars built was proportionally *greater* in areas of high male density (P. Backwell, unpublished work).

Second, we looked for the existence of two classes of males. A common problem in many studies is deciding whether the separation of individuals into two classes is biologically valid when the defining criterion is presence or absence of a behaviour. Our results suggest that the number of males not building pillars did not differ significantly from that expected by chance. Closer analysis of the data suggests, however, that males may be in two phases with respect to pillar-building. The only measured variable that differed between P-males and NP-males was the number of days they were seen on the surface. Data from P-males suggests that the number of days present is unrelated to the rate of pillar building (pillars/day). The observed variation in the rate of pillar-building thus suggests that some males were building more, and others fewer, pillars than expected. The fact that the percentage of P-males did not increase indicates that only some males were influenced by the additional food. In conclusion, the number of males that did not build pillars is not greater than that expected by chance, so we reject the hypothesis that there is a genuine class of non-pillar-builders. However, the lack of change in the percentage of males building pillars between treatments suggests that males vary in their propensity to build pillars through time.

Third, our results suggest that there are costs associated with pillar-building. Food supplementation, which presumably raises the ability of males to incur

energetically expensive behaviour, had several significant effects on pillar-building. Most notable was the two-fold increase in the number of pillars built. This appeared to be due to increased levels of pillar-building by a subset of the males present (operationally defined as P-males). While the number of pillars built increased, the percentage of males building pillars did not ($P=0.09$). With food supplementation more males were present on the surface each day. However, P-males did not spend significantly more days on the surface in the presence of food. Instead they build more pillars and the time between bouts of pillar-building decreased.

Pillars as signals: male quality or sensory exploitation?

The most common costs of preferred male traits are energetic (Höglund et al. 1992) or due to increased predation risk (Ryan 1985). If costs are energetic, ornamentation should increase with greater access to food (Evans 1991). Our data suggest that pillars may act as indicators of male quality. Pillar-building fits two predictions of handicap models. First, pillars are probably reliable indicators of a male's vigour, in as much as they reflect the ability to exploit food in the current environment (Kodric-Brown and Brown 1984). Second, there is non-random mating due to female choice because a male with a pillar is more likely to attract a mate (Christy 1988b). Unfortunately, evidence that the magnitude of a trait reflects male condition or parasite load is not conclusive evidence that it evolved through the handicap process (Kirkpatrick and Ryan 1991). Even breeding experiments showing heritability of ornamentation and positive effects of mate choice on offspring fitness do not distinguish between the two models of co-evolution (e.g., Norris 1993). Heritable viability, and a correlation between viability and ornamentation may also be the outcome of Fisherian runaway (Balmford and Read 1991).

Behavioural evidence from *Uca beebei* strongly implicates sensory exploitation in the evolution of pillar-building. First, females do not discriminate between burrows with and without pillars after entering them. This suggests that non-random mating is due to passive attraction (*sensu* Arak 1988). If females regard pillars as a signal of male quality, we would expect them to remain in burrows with pillars more often than those without. This is not the case ($G=1.53$, $n=155$ males, $P>0.1$; J.H. Christy, unpublished work). Second, experiments show that females preferentially enter burrows with pillars when exposed to an artificial predator (Christy 1988b). Is this evidence sufficient to demonstrate that pillars are products of sensory exploitation? While suggestive, the answer is probably not. In fact, there is evidence compatible with three other models for female choice. Pillars could be prod-

ucts of: (1) the handicap process: because food affects pillar-building and, on average, males with pillars should be more viable; (2) the Fisherian process: because "runaway" is halted when preferred traits become costly; (3) direct selection: males with pillars are probably better fed and, if this acts an indicator of parasite levels or risk of disease transfer, females may gain direct benefits by choosing males with pillars (Reynolds and Gross 1990). To date, the only direct benefit that has been looked for is a relationship between pillars and burrow quality; none was found (J. H. Christy, unpublished work).

Studies of the current selective value of traits provide limited information about their evolutionary history (Williams 1966; Gould and Vrba 1982; see Mumme 1992 for an applied example). Only the assumption that all traits that confer a selective advantage evolved for their present function justifies determining evolutionary history from current selective value. That this line of reasoning is risky is neatly illustrated by the outcome of the various "genetic" models of female choice. Here, three distinct evolutionary processes all predict the same possible outcome: a positive correlation between ornamentation and male condition. We should thus exercise caution before concluding that traits with these properties have evolved *because* they signal male quality.

The problem of explaining the evolution of ornaments seems overwhelming. We believe that the recent distinction noted by Reeve and Sherman (1993) highlights one key issue. They argue that adaptations can be explained either by an account of their selective history, or by investigating why a trait is maintained in the population at present. Maintenance of a trait is clearly open to investigation. In this study we have shown that pillar building is condition-dependent. Females mating with males with pillars seem to be more likely to mate with males in better condition. Females that do not show sensory biases such that they respond preferentially to males with pillar may thus lose out. In terms of its present function then, our results suggest that female choice for good genes or direct benefits may be responsible for the maintenance of pillar building. Distinguishing between these two explanations will require breeding experiments testing whether female choice increases offspring viability, or studies that look for direct benefits to females of mating with males with pillars. If neither occur, then genuine constraints on the sensory system, as envisaged by models of sensory exploitation, may explain pillar building.

Finally, we note that our results are somewhat surprising because pillar building does not look like a costly activity, far less one that is condition-dependent. A similar result has been documented in great snipe (*Gallinago media*) where the amount of white on the tail may be limited by environmental conditions (Höglund et al. 1992). In both studies the proximate

mechanisms constraining the expression of a preferred male trait are unknown. At present there are few experimental studies of the costs associated with ornaments. More are needed, especially those that attempt to link differential costs with male quality.

References

Arak A (1988) Female mate selection in the natterjack toad: active choice or passive attraction. Behav Ecol Sociobiol 22: 317–327

Balmford A, Read AF (1991) Testing alternative models of sexual selection through female choice. Trends Ecol Evol 6: 274–276

Balmford A, Thomas ALR, Jones IL (1993) Aerodynamics and the evolution of long tails in birds. Nature 361: 628–631

Basolo AL (1990) Female preference predates the evolution of the sword in swordtail fish. Science 250: 808–809

Bennet-Clark HC, Ewing AW (1967) Stimuli provided by courtship of male *Drosophila melanogaster*. Nature 215: 669–671

Christy JH (1988a) Pillar function in the fiddler crab *Uca beebei* (I): effects on male spacing and aggression. Ethology 78: 53–71

Christy JH (1988b) Pillar function in the fiddler crab *Uca beebei* (II): competitive courtship signalling. Ethology 78: 113–128

Christy JH, Salmon M (1991) Comparative studies of reproductive behavior in mantis shrimps and fiddler crabs. Am Zool 31: 329–337

Crane J (1975) Fiddler crabs of the world, Ocypodidae, genus *Uca*. Princeton University Press, Princeton

Enquist M, Arak A (1993) Selection for exaggerated male traits by female aesthetic preferences. Nature 351: 446–448

Evans MR (1991) The size of adornments of male scarlet-tufted malachite sunbirds varies with environmental conditions, as predicted by handicap theory. Anim Behav 42: 797–803

Grafen A (1990a) Sexual selection unhandicapped by the Fisher process. J Theor Biol 44: 475–516

Grafen A (1990b) Biological signals as handicaps. J Theor Biol 144: 517–546

Gould SJ, Vrba E (1982) Exaptation: a missing term in the science of form. Paleobiology 8: 4–15

Höglund J, Kalas JA, Fiske P (1992) The costs of secondary sexual characters in the lekking great snipe (*Gallingo media*). Behav Ecol Sociobiol 30: 309–315

Iwasa Y, Pomiankowski A, Nee S (1991) The evolution of costly mate preferences. II. The handicap principle. Evolution 45: 1431–1442

Jennions MD (1993) Female choice in birds and the cost of long tails. Trends Ecol Evol 8: 230–232

Kirkpatrick M (1982) Sexual selection and the evolution of female choice. Evolution 36: 1–12

Kirkpatrick M, Ryan MJ (1991) The evolution of mating preferences and the paradox of the lek. Nature 350: 33–38

Kodric-Brown A, Brown JH (1984) Truth in advertising: the kinds of traits favoured by sexual selection. Amer Nat 124: 309–323

Lande R (1981) Models of speciation by sexual selection on polygenic traits. Proc Natl Acad Sci USA 78: 3721–3725

Marchetti K (1993) Dark habitats and bright birds illustrate the role of the environment in species divergence. Nature 362: 149–152

Meyer A, Morissey JM, Schartl M (1994) Recurrent origin of a sexually selected trait in *Xiphophorus* fishes inferred from a molecular phylogeny. Nature 368: 539–542

Møller AP (1994) Sexual selection and the barn swallow. Oxford University Press, Oxford

Mumme RL (1992) Do helpers increase reproductive success? Behav Ecol Sociobiol 31: 319–328

Norris K (1993) Heritable variation in a plumage indicator of viability in male great tits *Parus major*. Nature 362: 537–539

Pomiankowski A (1994) Swordplay and sensory bias. Nature 368: 494–495

Pomiankowski A, Sheridan L (1994) Linked sexiness and choosiness. Trends Ecol Evol 9: 242–244

Pomiankowski A, Iwasa Y, Nee S (1991) The evolution of costly mate preferences. I. Fisher and biased mutation. Evolution 45: 1422–1430

Proctor HC (1991) Courtship in the water mite *Neumania papillator*: males capitalise on female adaptations for predation. Anim Behav 42: 589–598

Proctor HC (1992) Sensory exploitation and the evolution of male mating behaviour: a cladistic test using water mites (Acari: Parasitengona). Anim Behav 44: 745–752

Reeve HK, Sherman PW (1993) Adaptation and the goals of evolutionary research. Q Rev Biol 68: 1–32

Reynolds JD, Gross MR (1990) Costs and benefits of female mate choice: is there a lek paradox? Am Nat 136: 230–243

Ryan MJ (1985) The Tungara frog. University of Chicago Press, Chicago

Ryan MJ (1990) Sexual selection, sensory systems and sensory exploitation. Oxford Surv Evol Biol 7: 157–195

Ryan MJ, Keddy-Hector A (1992) Directional patterns of female mate choice and the role of sensory biases. Am Nat 139: S4–S35

Ryan MJ, Rand AS (1993) Sexual selection and signal evolution: the ghost of signals past. Proc Roy Soc B 340: 187–195

Siegel S, Castellan NJ Jr (1988) Nonparametric statistics for the behavioral sciences. MacGraw-Hill, New York

Sutherland WJ, De Jong MCM (1991) The evolutionary stable strategy for secondary sexual characters. Behav Ecol 2: 16–20

Weary DM, Guilford TC, Weisman RG (1993) A product of discriminative learning may lead to female preferences for elaborate male traits. Evolution 47: 333–336

Williams GC (1966) Adaptation and natural selection. Princeton University Press, Princeton

Zahavi A (1977) The cost of honesty: further remarks on the handicap principle. J Theor Biol 67: 603–605

Zeil J, Nalbach G, Nalbach HO (1986) Eyes, eye stalks and the visual world of semi-terrestrial crabs. J Comp Physiol A 159: 801–811