SUCCESSFUL FATHERS SIRE SUCCESSFUL SONS

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Abstract.—The theory of sexual selection holds a central role in evolutionary biology. Its key assumption is the heritability of traits associated with reproductive success. Strong indirect evidence supporting this assumption comes from the numerous studies that have identified heritable traits associated with mating success. However, there remain only a handful of studies that have attempted to demonstrate directly that successful fathers have successful sons. We present the results of an experimental study of the mating success and phenotype of male field crickets *Gryllus bimaculatus* (Orthoptera: Gryllidae) and their offspring. These reveal that sons of successful males obtain significantly more copulations than sons of unsuccessful males. There was no difference in body size of sons of either group, but sons of successful males had significantly longer development times. This may represent a naturally selected cost to traits associated with success that could balance their sexually selected advantages.

Key words.—Competition, female choice, *Gryllus bimaculatus,* heritability, mating, sexual selection, trade-off.

A key assumption of sexual selection theory is the heritability of traits associated with reproductive success. Numerous studies have identified traits associated with male mating success (Andersson 1994; Bakker and Pomiankowski 1995), ranging from morphological features such as weapons (Clutton-Brock et al. 1979; Conner 1988), ornaments (Andersson 1982; Møller 1988), and body size (Arak 1983; Deutsch et al. 1990) to various behavioral characters (Ryan 1980; Höglund and Lundberg 1987). Several studies have also shown that such traits are heritable: body size (Simmons 1987a) and calling bout length (Hedrick 1988) in crickets, song and morphology in grasshoppers (Butlin and Hewitt 1988), territoriality in fruitflies (Hoffmann 1991), and male coloration in guppies (Houde 1992).

Although these studies provide strong indirect evidence for the heritability of male mating success, there remains a dearth of studies that directly demonstrate that successful fathers have successful sons. Apart from the intrinsic value of direct evidence, it is important to make this step. Success is likely to be the result of a combination of traits, each with different effects (positive or negative) and heritabilities (Kirkpatrick 1982; Wilkinson 1987; Ryan 1997). Selection acts on these traits through female choice and male-male competition, both of which may involve several characters. Females have been shown to use multiple traits in mate assessment (e.g. Zuk et al. 1990; Koderic-Brown 1993; Brooks and Caithness 1995), and the outcome of male-male competition may also depend on more than one trait (e.g., Clutton-Brock 1988). Difficulties in identifying all traits affecting mating success are compounded by the problem of establishing an unequivocal causal relationship between a particular trait and success itself. Because selection acts on success,

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not directly on traits, we can gain insights into the process of sexual selection by examining mating success itself without explicitly identifying the traits involved.

The field cricket, *Gryllus bimaculatus,* is widely distributed in southern Europe, where it frequently occurs at high densities. Males fight over and defend burrows and attract receptive females by calling. Females choose between males on the basis of calling song (Simmons 1988a), and the mating system also involves direct male competition with fierce fighting between males (Simmons 1986). Females cannot be coerced into mating because they must actively mount the male and allow him to attach a small spermatophore. Song characteristics are correlated with male size, which is heritable in *G. bimaculatus* (Simmons 1987a). Both traits are associated with male reproductive success, but whether sons of successful fathers have a mating advantage has not been investigated. Using a design that allows for both male-male competition and female choice, we investigate whether males successful in obtaining matings in competition with a rival male sire sons displaying their father's mating advantage.

MATERIALS AND METHODS

Crickets were taken from a 30-year-old laboratory culture established from a single wild population and bulk reared at 29°C and 18:6 L:D cycle. Males and females were 10-days-old on the day of the experiment and had been housed individually in 9-cm pots since their penultimate instar. The males used in each mating trial were mated to a nonvirgin female prior to the onset of the experiment to ensure that they were capable of successfully transferring a spermatophore and to minimize variation in sexual experience.

Two males weighed to the nearest milligram were released simultaneously into a 30 × 30 cm arena containing a 10-day-old virgin female. The female was allowed contact with both males, but was initially prevented from mating with either (by restricting her under a plastic cover) until they had both begun courtship singing, thus indicating they had a spermatophore ready. Male crickets produce a spermatophore prior to mating and only engage in courtship song if they have a spermatophore ready (Huber 1962). The female was then released from the plastic cover, thus allowing access to both males, and allowed to copulate with one of them (a process taking < 1 min). The unsuccessful male was removed from the arena 5 min later.

A few females mated with one male and then immediately mated with the other. This resulted in physical displacement of the first male's spermatophore when the second male attached his own spermatophore. In all cases this happened before sperm transfer from the first male's spermatophore had begun (< 5 min). The second male to mate in these cases was deemed successful because his spermatophore remained attached to the female for at least 40 min., and therefore allowed sperm transfer (Simmons 1987b). Males whose spermatophores were displaced could not immediately remate because they require a regeneration time of about an hour between matings before being able to produce a new spermatophore and mate again (Simmons 1988a), by which time the spermatophore from the second male had been drained of sperm. Females never removed spermatophores before

they had drained of sperm or consumed spermatophores in this study. This contrasts with the finding of a previous study (Simmons 1988b), possibly due to differences in food quality.

The female was allowed to mate again with the successful male after an hour because singly mated females have low egg-hatching success (Simmons 1988b). The unsuccessful male was paired with another 10-day-old virgin female and allowed to mate twice with her. The successful male was paired again the next day to a new 10- day-old virgin female and mated with her twice. Thus, successful males mated in total five times: once before the experiment, twice to the female in the mating trial, and twice the following day to another female allocated to him. The unsuccessful male mated three or four times: once before the start of the experiment, occasionally once to the female during the mating trial (see above), and twice to a female allocated to him at the end of the mating trial. The amount of sperm in subsequent spermatophores does not decline over at least five matings in individual males (Simmons 1987b). This triplet design provides females mated to males designated as either "successful" (S), "successful allocated" (S[a]), or "unsuccessful" (U[a]) (Fig. 1). This design allows us to examine the possibility that females that can choose between two males may allocate more resources to offspring. Choice per se has been show to influence the proportion of available eggs laid in *G. bimaculatus* (Simmons 1987c). All three females in each mating triplet were matched for size (ANOVA $F_{(2,39)} = 1.67, P = 0.20$). In total, 14 triplets, involving 42 females, were performed.

The female from each mating trial was placed in an individual container and provided with food, water, and sand for egg laying. After three days the female was removed, the number of eggs laid was counted, and eggs were placed on damp cotton wool in a petri dish and incubated at 29°C until hatching. The first 50 nymphs from each female were placed together in a 13-liter plastic box and provided with food and water. Development time, body weight, and pronotum width of the first 10 males to reach adulthood were recorded. These 10 males were tested in mating trials against the offspring of the two other females from the same mating triplet (two trials/male; 30 trials/triplet; Fig. 1). Three of the original 14 triplets were not used because one or more females failed to produce a sufficient number of offspring. In total, 10 male offspring from each of 33 females of 11 triplets were used in 324 mating trials (3 male offspring escaped). Males were scored as being successful or unsuccessful in the same way as their fathers. Males were randomly allocated with respect to previous trials. All virgin females used in the mating trials were unrelated to the males. Mating trials of sons were carried out without knowledge of paternal mating success. To determine whether the outcome of contests between sons were repeatable, 24 randomly chosen mating trials were repeated in the same way after six days.

RESULTS

Males obtaining copulations were not significantly heavier than unsuccessful males (paired *t*-test, $t = 1.844$, df = 13, $P = 0.088$). Sons of successful males were more successful in obtaining copulations than sons of unsuccessful males

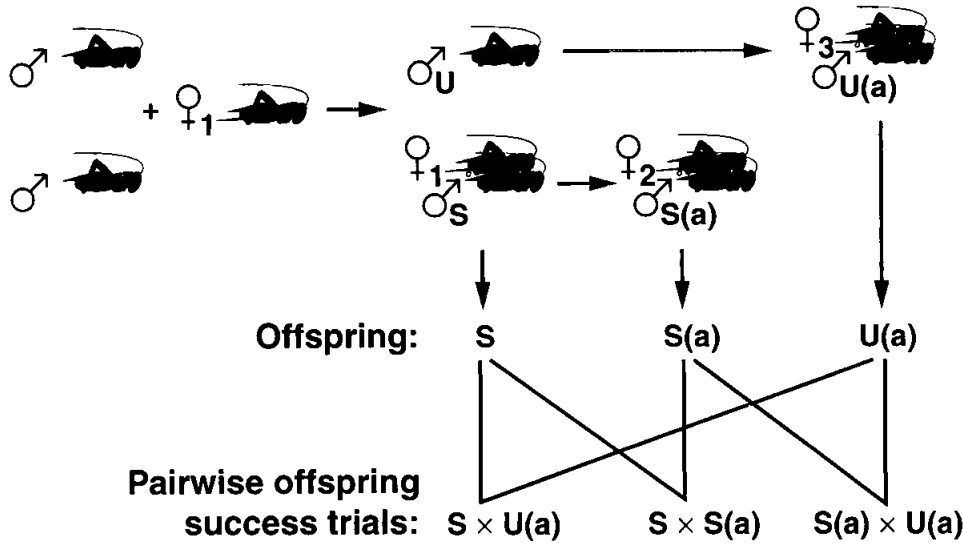## Pairwise paternal success trial:

FIG. 1.   FIG. 1. Experimental design (see Materials and Methods for detailed explanation). Two males were placed in an arena with a single virgin female. The female mated with one male, termed the "successful" male. The male failing to mate was termed the "unsuccessful" male. Both males were each subsequently allocated matings with another virgin female. The offspring of all three females were reared to adulthood. Those of the female mated in the initial trial are designated "successful" (S), those from the female allocated to the successful male are designated "successful allocated" (S[a]), and those of the female allocated to the unsuccessful male are designated "unsuccessful allocated" (U[a]). A male from each offspring group: S, S(a), and U(a), was placed in an arena with a male from one of the other two groups and a virgin female, and the male gaining the mating was noted (as in the paternal trial). Ten males from each offspring group each took part in two trials with males from each of the two groups. This entire protocol was repeated for 11 original mating trials, giving 330 (11 × 30) offspring trials in total.

(combined chi square [Snedecor and Cochran 1967, p. 253]: S vs. U[a], $\chi^2 = 4.24$, $P < 0.05$; S[a] vs. U[a]], $\chi^2 = 4.43$, $P < 0.05$; S vs. S[a]), $\chi^2 = 1.19$, $P > 0.2$; df = 11 for each of the three combinations); (Fig. 2, Table 1). Copulation success was highly repeatable: 22 of 24 trials repeated six days apart yielded the same result.

Sons successful in obtaining copulations did not tend to be heavier than unsuccessful ones (S vs. U[a], paired t-test, $t = 1.07$, df = 107, $P = 0.29$; S[a] vs. U[a] $t = 1.67$, df = 107, $P = 0.097$), unless both males shared the same father

(S vs. S[a], $t = 4.42$, df = 107, $P = 0.0001$). There was no difference in body weight between sons of successful or unsuccessful fathers (repeated measures ANOVA: male category, $F = 1.09$, df = 2, $P = 0.35$; repeat $F = 1.15$, df = 9, $P = 0.34$; interaction $F = 0.76$, $P = 0.67$; successful sons: mean 0.718 ± 0.024 g [SE], $n = 110$; successful allocated sons: mean 0.754 ± 0.020 g $n = 110$; unsuccessful sons: mean 0.746 ± 0.026 g, $n = 110$). Nor was there any difference in pronotum width (repeated measures ANOVA: male category, $F = 1.94$, df = 2, $P = 0.16$; repeat $F = 1.29$, df = 9, $P = 0.269$; interaction $F = 0.90$, $P = 0.53$; successful sons: mean 6.84 ± 0.038 mm [SE], $n = 110$; successful allocated
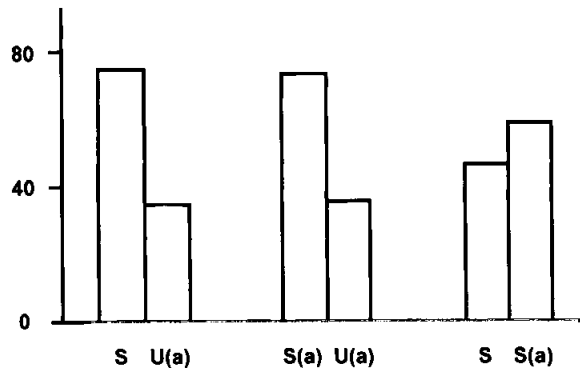
Total number of matings

FIG. 2.   Frequency histograms of total number of matings obtained by sons of successful (S), unsuccessful allocated (U[a]), and successful allocated (S[a]) fathers. Males that are successful in obtaining matings have sons that are more likely to be successful themselves compared to sons of unsuccessful fathers.

TABLE 1.   Data from the eleven triplets of mating trials. Each triplet involves 30 pairwise trials in which sons of "successful" (S), "unsuccessful allocated" (U[a]), or "successful allocated" (S[a]) fathers were placed together with a female until one of them mated with her. Results indicate the number of occasions on which a male from either group was successful in mating.

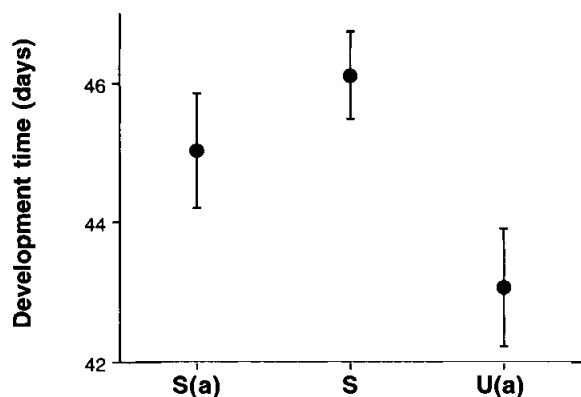| S vs. U(a)	S(a) vs. U(a)	S vs. S(a)
7:3	9:1	3:7
7:3	9:1	3:7
8:2	8:2	3:7
6:2	6:2	2:6
8:2	9:1	3:7
7:3	4:6	7:3
7:3	7:3	5:5
8:2	4:6	3:7
6:4	7:3	6:4
6:4	7:3	8:2
6:4	7:3	5:5

FIG. 3. Successful males sire sons with longer development times than sons of unsuccessful fathers. Means ± 95% confidence limits. S(a), sons of successful allocated fathers ($n = 110$); S, sons of successful males ($n = 110$); U(a), sons of unsuccessful allocated males ($n = 110$).

sons: mean 7.01 ± 0.038 mm, $n = 110$; unsuccessful sons: mean 6.89 ± 0.044 mm, $n = 110$). However, sons of successful males had significantly longer development times than sons of unsuccessful males (repeated measures ANOVA: male category, $F = 3.41$, df $= 2$, $P = 0.045$; repeat $F = 14.72$, df $= 9$, $P = 0.0001$; interaction $F = 1.53$, $P = 0.131$; Fig. 3). This analysis is potentially pseudoreplicative because S and S[a] males share the same father. To confirm that the result is robust, we conducted ANOVAs for the three possible pairwise comparisons (repeated measures ANOVA, S vs. S[a]: male category, $F = 0.26$, df $= 1$, $P = 0.62$; repeat $F = 18.66$, df $= 9$, $P = 0.0001$; interaction $F = 1.31$, $P = 0.236$; S vs. U[a]: male category, $F = 5.50$, df $= 1$, $P = 0.036$; repeat $F = 12.13$, df $= 9$, $P = 0.0001$; interaction $F = 0.55$, $P = 0.86$; S[a] vs. U[a]: male category, $F = 4. 63$, df $= 1$, $P = 0.044$; repeat $F = 18.45$, df $= 9$, $P = 0.0001$; interaction $F = 0.09$, $P = 0.9$). This verifies the result of the combined ANOVA: offspring of successful males have longer development times.

DISCUSSION

Our study shows that successful fathers do indeed sire successful sons. This is unlikely to be the result of paternal nutrient contribution to offspring because females did not consume spermatophores in this study. Furthermore, the spermatophore of *G. bimaculatus* is small, with negligible effect on female fecundity (Simmons 1988b). Exposing females to two males as opposed to allocating a male did not affect sons' mating success, indicating that differences between sons of successful and unsuccessful males are not due to females responding to the possibility of choosing a mate by allocating additional resources to offspring. This also rules out the possibility that females choose mates with complimentary genotypes or to optimize outbreeding (Olsson et al. 1996a). By rearing individuals in family groups, sons of successful and unsuccessful fathers may have experienced differences in intensity of competition, which might affect development time and subsequent mating success. This possibility is remote because nymphs were provided with an excess of food and therefore were unlikely to compete for

food. Moreover, several studies have demonstrated effects of paternal genotypes despite rearing individuals in full-sib groups (e.g., Simmons 1987c; Norris 1993; Moore 1994; Jia and Greenfield 1997).

As is likely to occur in nature, our experimental design allowed both female choice and male-male competition to operate simultaneously (Wilkinson 1987). This will lead to more sexual traits being exposed to selection than in experiments examining single male traits. Previous studies have found that larger male field crickets tend to gain more matings (e.g., Simmons 1986). In our study, when paternal genotype was controlled by comparing the sons of the same male (S vs. S[a]), we also found a strong effect of male size. However, the outcome of trials between sons of successful and unsuccessful males could not be predicted on the basis of male size, indicating that there are multiple phenotypic trait differences between males. Male size is one such trait, but it appears to have been eclipsed by other heritable differences that make paternal success a better predictor of offspring success than size alone.

Previous studies examining the relationship between male mating success and offspring fitness provide ambiguous results. A number support the assumption of "good genes" sexual selection that male mating success is correlated with progeny fitness (e.g., Reynolds and Gross 1992; Møller 1994; Petrie 1994; Olsson et al., 1996b). In *Drosophila melanogaster*, male mating success correlates positively with offspring competitiveness (Partridge 1980; Taylor et al. 1987), although this effect is dependent on density (Wilkinson 1987). Similarly, in wax moths the relationship between sire attractiveness and offspring fitness varies depending on environmental conditions (Jia and Greenfield 1997). Other studies have failed to establish a relationship between offspring quality and male mating success (e.g., Boake 1985; Payne and Westneat 1988; Howard et al. 1994). Only a handful of studies have directly examined the relationship between mating success of fathers and sons. Attractiveness to females has been shown to be heritable in the southern green stinkbug (McLain and Marsh 1990), a lekking sandfly (Jones et al. 1998), and in cockroaches rejected males are more likely to have unattractive sons (Moore 1990). Particularly interesting, because it utilizes a measure of male mating success that allows both male-male competition and female choice, a quantitative genetic study of *D. melanogaster* (Hughes 1995) found no evidence for a "good genes" model of sexual selection, but did reveal significant additive genetic variance in male mating success. Not all studies of the possibility of heritability of male mating success have been affirmative. An apparently highly sexually selected species, the lekking Mediterranean fruit fly appears to show no heritable component of mating success between fathers and sons (Whittier and Kaneshiro 1995).

Why selection for traits conferring mating advantages does not rapidly exhaust genetic variation in such traits remains a major question (Maynard Smith 1985). It is suggested that heritabilities of sexually selected traits may have been overestimated in recent years (Alatalo et al. 1997), but there is little doubt that variation in sexual traits does exist and can have high heritability (Hedrick 1988; Houde 1992). In this study, heritability of male mating success could not be mea-

sured because males were ranked as either successful or unsuccessful. However, it is clear that mating success has a heritable component in *G. bimaculatus*. A number of solutions to the paradox of why heritability of fitness-related traits does not result in trait fixation have been proposed (Houle 1992; Andersson 1994; Pomiankowski and Møller 1995; Rowe and Houle 1996). It has recently been suggested that genetic variance in sexually selected traits can be maintained if such traits are condition dependent and thus influenced by many loci (Rowe and Houle 1996). Additionally, traits under directional selection may harbor greater variability because deviations from the mean of the trait in the direction of selection will be favored (Houle 1992). Sexually selected traits are more likely to be under directional selection due to mutation bias (Iwasa et al. 1991; Pomiankowski et al. 1991). Moreover, if directional selection is greater than linear, this will favor modifiers that act to increase genetic variance (Houle 1992; Pomiankowski and Møller 1995). Another class of explanations are based on the possibility of trade-offs between mating success and other fitness-related characters (Roff 1992). For instance, individuals with prominent sexual traits may be more successful in acquiring mates, but show reduced survival (Fisher 1958).

Our data suggest that a trade-off may occur in the field cricket. The sons of successful males are more successful themselves, but experience longer development times. Development time has costs in terms of increased generation time, which is of key importance in continuous breeders such as *G. bimaculatus*. Sons of successful males developed on average 2.6 days slower than sons of unsuccessful males. This represents approximately 5% of total generation time, a difference that would undoubtedly be associated with decreased fitness, both through reduced probability of survival to maturity and later onset of reproduction increasing generation time (Roff 1992). To what extent this is balanced by the higher mating success of these males is difficult to assess. Interestingly, despite achieving the same adult body mass, female *G. bimaculatus* have shorter development times than males (Tregenza and Wedell 1998). A negative genetic correlation between traits associated with mating success and development time may exist in the field cricket, thus aiding the maintenance of variation in traits affecting male mating success (Lande 1982; Rose 1982). This is similar to the situation in *Drosophila robusta*, where natural and sexual selection may also balance each other. In this species males carrying a certain karyotype enjoy higher mating success, but are disadvantaged by longer development times (Etges 1996). This contrasts with the absence of genetic correlations, negative or positive, between male fitness components in *D. melanogaster* (Hughes 1995) and the lack of trade-offs with male attractiveness found in the lekking sandfly (Jones et al. 1998).

Further investigation is required to determine to what extent the suggested trade-off between development time and mating success is genetic as opposed to phenotypic in *G. bimaculatus*. Regardless of the magnitude of any such trade-off, it is clear that although multiple traits are associated with male success, there is a detectable heritable component, thus supporting the fundamental assumptions of the theory of sexual selection.

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