Behaviour

Costs of mating with males possessing long tails in the female guppy

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Short title: Mating costs in female guppies

Summary

Males of the guppy <u>Poecilia reticulata</u> have longer tails (caudal fins) than females, and

the tail lengths of males show a high individual variation.   Female guppies in a

population exhibit mate preference on the basis of the total length of the males, and not

their tail lengths.   Therefore, the occurrence of long tails in male guppies has been

suggested as a deceptive tactic to attract females with fewer growth costs.   If males

possessing long tails would be cheater males, it is predicted that females would incur

costs through mating with the males having long tails.   In the present study, the costs

incurred by females as a result of mating with males possessing proportionally long tails

were examined.   Females that had mated with males possessing long tails delivered

fewer numbers of offspring than those that had mated with males possessing short tails.

After maturation, daughters of males with long tails exhibited smaller body sizes and

lower reproductive output than daughters of males having short tails.   On the other

hand, sons of the long-tailed males had greater total lengths on account of their longer

tails as compared with sons of the short-tailed males.   These results suggest that, by

mating with males possessing long tails, females not only incur costs with respect to the

decrease in growth and reproduction in their daughters but also obtain benefits in terms

of sexual attractiveness of their sons.   It is also conceivable that females might develop

some counter-adaptations to minimize the costs of mating with males having long tails.

Introduction

Sexual conflict between males and females has recently attracted a great deal of interest

among behavioral and evolutionary ecologists (Chapman et al., 2003; Zeh & Zeh, 2003;

Arnqvist & Rowe, 2005).   In the last decade, sexual conflict has been investigated

from many aspects of reproductive ecology (Magurran & Seghers, 1994; Brown et al.,

1997; Miller, 2003; Maklakov et al., 2005), particularly from the viewpoint of sexual

selection (Eberhard & Cordero, 2003; Kokko et al., 2003; Zeh & Zeh, 2003; Arnqvist &

Rowe, 2005).

In general theories of sexual selection, females often choose high-quality males as their mates (Andersson, 1994; Ryan, 1997). Since it is considered that high-quality males provide the females with high-quantity and/or quality resources or they possess good genes, the females can thus obtain direct or indirect benefits by mating with high- quality males. Hence, female mate preference might have evolved based on the choice of particular male traits that indicate the males' quality (Andersson, 1994; Ryan, 1997).

On the other hand, the evolution of male deceptive tactics against female mate preferences under certain circumstances has been theoretically predicted (Weldon & Burghardt, 1984; Dawkins & Guilford, 1991; Johnstone & Grafen, 1993; Kokko, 1997). Several empirical studies have suggested that, in some cases, males, including those of low quality, attempted to deceive females by assuming appearances similar to those of high-quality males in order to mate with the females (Candolin, 1999; Backwell et al., 2000). It is conceivable that females often incur costs by mating with the cheater males (Weldon & Burghardt, 1984; Johnstone & Grafen, 1993; Johnstone, 1997). If

the costs of being deceived incurred by the females are great, counter-adaptations by the females against male deception would occur.   These counter-adaptations would include discriminating the cheater males or ceasing mate choice on the basis of the male traits that include male deception (Weldon & Burghardt, 1984; Johnstone & Grafen, 1993). It can be considered that this female-male interaction is a form of sexual conflict. However, the costs to females that are deceived by cheater males have not yet been empirically demonstrated.   In the present study, we aimed at examining the costs incurred by females when they mate with possible cheater males in the guppy, <u>Poecilia reticulata</u>.

The guppy is a live-bearing poeciliid fish native to the streams of Trinidad and adjacent parts of South America (Houde, 1997).   The guppy shows remarkable sexual dimorphism and dichromatism; males have longer fins than females and assume brightly colored spots on their bodies.   It is well known that females choose their mates on the basis of male secondary sexual traits such as orange spot patterns (Houde, 1987; Kodric-Brown, 1989).   Male guppies have longer tails (caudal fins) than female guppies, and the tail lengths of males show a high individual variation (Bischoff et al.,

1985; Karino & Matsunaga, 2002).   Although Bischoff et al. (1985) have documented

female mate preference on the basis of the male tail size, Karino & Matsunaga (2002)

have indicated that female guppies choose their mates on the basis of male total length,

and not tail length alone.   Thus, females do not use male tail length as either the

criterion for mate choice or as an indicator of male quality.   This suggests that some

mechanism different from the indicator mechanism (Andersson, 1994) may have

resulted in the evolution of the long tails in male guppies.

Since it is possible that males have the ability to increase their tail lengths

with fewer growth costs than those required for body production (cf. Basolo, 1998),

they can achieve larger total lengths by tail elongation with fewer costs.   On the other

hand, Reynolds & Gross (1992) have revealed indirect benefits of female mate

preference for males having larger total lengths, i.e., offspring of larger males grew

faster and their daughters reproduced to a greater extent.   The indirect benefits of

mating with larger males may reflect the inheritance of larger body sizes by the

offspring.   However, in the case of females mating with males having larger total

lengths but smaller body sizes (standard lengths) and longer tails, it can be expected that

the true body sizes of their offspring would not be larger, and the reproductive output of

their daughters would be lower.   This suggests that mating with males possessing long

tails may reduce the indirect benefits to females.

Therefore, some of the costs incurred by females by mating with males

possessing long tails can be predicted as follows.   (1) By mating with males having

longer tails, the body sizes of their offspring would be smaller than those of the

offspring of males with shorter tails.   Particularly, the smaller body sizes would be

expected for daughters of the males with longer tails because female guppies do not

elongate their tails.   (2) The reproductive output of daughters of the males possessing

longer tails would be lower, probably due to their smaller body sizes.   These

assumptions were analyzed by a laboratory experiment in which guppies were reared

through three generations.

Methods

We used laboratory-reared descendants of feral guppies from the Hiji River (26˚43'N,

128˚11'E), Okinawa Island, southern Japan.   Guppies that are introduced into new

habitats exhibit flexibility in changing their appearances and life history components

accumulated over several years to suit the new environment (Endler, 1980; Reznick et

al., 1990).   Since guppies were introduced into Okinawa in the 1970s, they might have

been subjected to natural and sexual selection for a sufficiently long duration to enable

adaptation to the new habitats (Karino & Haijima, 2001).   Karino & Matsunaga (2002)

have documented that female guppies in this population choose their mates on the basis

of male total length.

Guppies were reared in 40-l aquariums with circulated water maintained at

25˚C-28˚C with a 12 h light: 12 h dark photoperiod in a laboratory at the Tokyo

Gakugei University.   They were fed newly hatched brine shrimp nauplii and

commercial flake food (Tetramin; Tetra Werke, Germany) daily.

Preparation of parental individuals

We chose a pair of parental (P) males that had similar total lengths (<1 mm difference) but different tail lengths (>2 mm difference) from the stock aquariums. We prepared 20 male pairs with different individuals. The males of the pairs who had long tails (long-tailed males) exhibited significantly longer tails and smaller standard lengths than the other males (short-tailed males), but the difference in total lengths was not significant (Table 1).

In order to minimize the genetical effect of P females on their offspring (F1), we used a pair of virgin females of full siblings from a single brood to mate with a pair of the P males with different tail lengths. Considering that guppies fertilize internally, in order to obtain full siblings, fertilization had to be controlled and the virgin females had to be maintained separately from males from 4-5 weeks after birth. Four to five weeks after birth, the young fish expressed secondary sexual traits, such as male gonopodium (Houde, 1997), and the sex of individual fish could be determined based on these traits. Four months after birth, a virgin female and a given male were reared in an isolation tank until the female became pregnant. The fry of a single brood were

reared for 4-5 weeks in an aquarium, and fed with newly hatched brine shrimp nauplii

and the commercial flake food daily.   After sex determination at 4-5 weeks after birth,

females from a single brood were reared in an aquarium separately from males.   Four

months after birth, we chose a pair of P females with similar body sizes from a single

brood.   Twenty pairs of the P females were prepared from 20 full siblings from

different parents.   No significant difference in the total length, standard length, and tail

length was observed between the P female pairs (Table 1).

Collection and growth of F1

One individual of a pair of P females was reared with a long-tailed male from a pair of P

males in a tank (14 × 14 × 10 cm).   The other P female was reared with a short-tailed

male of the paternal pair in a different tank.   When the females became pregnant, the

males were removed from the tanks.   Immediately after the females delivered their

offspring (F1), the number of the offspring was counted.   The F1 offspring were

transferred and reared in isolation tanks ($14 \times 14 \times 10$ cm) at the same individual

density (200 cm^3/individual).   They were fed newly hatched brine shrimp nauplii and

the commercial flake food daily.   To minimize the effect of the food quantity on their

growth, we adjusted the amount of food provided as 0.02 mg of the flake food and 0.5

ml of water containing brine shrimp nauplii per individual per day.   Since the fry was

frail immediately after birth, we measured the total length of each offspring to the

nearest 0.1 mm using a vernier caliper 10 days after their birth.   The fish were

anesthetized with 0.06% 2-phenoxyethanol solutions during 2-3 min prior to

measurement.   The mean total length of the fry from a single brood was calculated for

further analysis.

In order to minimize the influence of reproductive investment, such as female

pregnancy and male courtships, on growth, the male and female F1 offspring were

reared separately 4-5 weeks after birth, i.e., before sexual maturation.   After complete

maturation, on 120 days after birth, we measured the total length, standard length, and

tail length of each fish to the nearest 0.1 mm using a vernier caliper.   Prior to

measurement, the fish were anesthetized with 0.06% 2-phenoxyethanol solutions.

Since the guppies are sexually dimorphic (Houde, 1997), the mean values of the total,

standard, and tail lengths of F1 males and females from a single brood were calculated.

The number, and mean body and tail lengths of F1 offspring were compared

between those from the P male pairs by paired $\underline{t}$-test, because all of data showed a

normal distribution (Kolmogorov-Smirnov one-sample test, $\underline{p} > 0.5$).

Reproductive output of F1 females

Following the measurement of body and tail size at 120 days after birth, we chose two

F1 females from a single brood whose lengths were closest to the mean standard length

of the females of the brood.   Subsequently, we paired F1 females from different

mothers of the same strain, i.e., an individual of the F1 females of a pair had a given P

mother that was a sister of the P mother of the other F1 female of the pair.   In order to

minimize the effect of males on the degree of reproductive output of F1 females, two F1

females of a pair were mated with the same male.   Each F1 female was separately

reared in an isolation tank ($14 \times 14 \times 10$ cm).   A given male was introduced into one of

the isolation tanks that contained a F1 female.   Three days after the introduction, the

male was transferred to the other tank that contained the other F1 female of the pair.

This male transfer between the two tanks was repeated until both the F1 females

became pregnant.

Immediately after the F1 females delivered their offspring (F2), the F1

females were removed from the tanks, and the number of F2 offspring was counted.

Ten days after birth, the total lengths of the F2 offspring were measured by the same

method used for the F1 offspring.   The mean total length in a single brood was

calculated.

We adopted parametric tests because all of data showed a normal distribution

(Kolmogorov-Smirnov one-sample test, $p > 0.2$).   The number and mean total length

of F2 offspring who were descendants from a pair of the long- and short-tailed P males

were analyzed by paired t-test.   Body sizes of the F1 females differed between the

pairs (see Results).   The influence of female body sizes on their reproductive output

could be expected (Abrahams, 1993).   Therefore, we also conducted ANCOVA using

the body sizes (standard length) of F1 females immediately prior to the delivery as a

covariate, the number or total length of F2 offspring as a dependent variable, and the

classification of P males (long- or short-tailed males) as a factor.

StatView 5.0 software (SAS Institute, USA) was used for statistical analysis.

Results

<u>Number and growth of F1 individuals</u>

P females that had mated with the long-tailed males produced fewer F1 offspring than P

females that had mated with the short-tailed males (paired $\underline{t}$-test, $\underline{t}_{19}$ = -2.8, $\underline{p}$ = 0.01;

Figure 1a).　Total lengths at 10 days after birth did not significantly differ between F1

offspring of the long- and short-tailed P males ($\underline{t}_{19}$ = 1.2, $\underline{p}$ = 0.28; Figure 1b).

Hundred and twenty days after birth, F1 males of the long-tailed P males

showed greater total lengths than those of the short-tailed P males (Table 2).　However,

standard lengths did not significantly differ between the F1 males of the long- and

short-tailed P males (Table 2).　The difference in the total lengths appeared to be due to the difference in tail lengths, i.e., F1 males of the long-tailed P males had longer tails than those from the short-tailed P males (Table 2).

The total and standard lengths of the F1 females of the long-tailed P males were significantly smaller than those of the short-tailed P males (Table 2) at 120 days after birth.　The difference in tail lengths between F1 females of the long- and short-tailed P males was not significant (Table 2).

Reproductive output of F1 females

In 36 pair broods from 18 experimental P pairs, F1 females produced F2 offspring.　F1 females that were daughters of the long-tailed P males delivered fewer F2 offspring than F1 females of the short-tailed P males (paired $\underline{t}$-test, $\underline{t}_{35} = -6.2$, $\underline{p} < 0.001$; Figure 2a). This difference in the number of F2 offspring was caused by both the difference in body sizes of F1 females (ANCOVA; body size of F1 female, $\underline{F}_{1,\,69} = 13.6$, $\underline{p} < 0.01$) and the

effect of their fathers (classification of P males, $F_{1, 69} = 7.1$, $p = 0.01$; Figure 3a).

At 10 days after birth, the mean total length of F2 offspring that were

descendants of the long-tailed P males was significantly smaller than that of F2

offspring from the short-tailed P males (paired t-test, $t_{35} = -3.7$, $p < 0.001$; Figure 2b).

However, no significant effect on the total length of F2 offspring was detected for body

sizes of F1 females (ANCOVA; $F_{1, 69} = 2.1$, $p = 0.15$) or classification of P males ($F_{1, 69}$

$= 1.7$, $p = 0.19$; Figure 3b).

Discussion

In accordance with our prediction, the results of this study indicate that mating with

males possessing proportionally long tails results in females incurring costs with respect

to growth and reproduction in their daughters. At 120 days after birth, daughters of

males possessing longer tails had smaller body sizes as compared with daughters of

males with shorter tails. The daughters of males having longer tails also exhibited

lower reproductive output, i.e., fewer offspring with smaller body sizes, than the

daughters of males with shorter tails.   The fewer number of offspring of the daughters

of long-tailed males was a result of their smaller body sizes.   These costs of mating

with males possessing long tails to females may evoke a sexual conflict between female

and male guppies.

In this guppy population, females choose their mates on the basis of male total

length, and it has been suggested that tail elongation in some male guppies is a

deceptive tactic to achieve large total length and to attract females (Karino &

Matsunaga, 2002).   The results of this study clearly showed that as a result of mating

with males possessing proportionally long tails females incur costs with regard to the

growth and reproduction of their daughters.   Therefore, it appears that male guppies

possessing long tails may act as "cheater" males in the case of females having a mate

preference for males with large total length.   In the green swordtail <u>Xiphophorus</u>

<u>helleri</u> (Rosenthal & Evans, 1998) and the sailfin molly <u>Poecilia latipinna</u> (MacLaren et

al., 2004), it is also known that females choose their mates on the basis of the apparent

size (body size plus fin size) of males and not by fin size alone.   Thus, it is probable

that in other poeciliid fishes with sexual dimorphism in fin size, a greater male fin size

is also a deceptive tactic to attract females.

Theoretical models have predicted the occurrence of counter-adaptations in

females when the costs of females on being deceived by cheater males are greater

(Weldon & Burghardt, 1984; Johnstone & Grafen, 1993).   The costs to female guppies

that are deceived by cheater males with long tails, such as the decrease in growth and

reproduction in their daughters, appear to be significant with regard to the females'

fitness.   Hence, it is possible that female guppies might develop some counter-

adaptations against male deception.   In fact, Karino & Kobayashi (2005) have

suggested that female guppies could discriminate tail lengths of males during the course

of mating by physical contacts with males.   At the first stage of the mating sequence

(orient response; Brooks & Caithness, 1995), females did not discriminate tail lengths

of males (Karino & Kobayashi, 2005), which is similar to the result of a dichotomous

female choice experiment in which females choose males through a clear glass partition

(Karino & Matsunaga, 2002).   However, at the subsequent stage of mating (gliding

response; Brooks & Caithness, 1995) with physical contacts between females and males,

females responded with a lower frequency to males with longer tails than those with

shorter tails (Karino & Kobayashi, 2005). The discrimination by the females against

male tail length may be a counter-adaptation against the deceptive tactic involving the

exhibition of long tails by males. It is also possible that, as documented in this study,

the smaller degree of clutch sizes of females that had mated with males possessing long

tails is another counter-adaptation of females. Females that mated with males having

long tails may manipulate their clutch sizes to a small degree in order to enhance the

investment in the next clutch that would be produced by mating with other mates.

On the other hand, in contrast with our prediction, sons of males having

longer tails did not show smaller standard lengths as compared with those of males with

shorter tails. Moreover, the sons of the long-tailed males exhibited greater total

lengths on account of their longer tails. Therefore, by mating with males possessing

long tails, females may be able to obtain indirect benefits, namely, a greater sexual

attractiveness of their sons to females. The possible benefit (sons with large total

lengths) may compensate, to a certain degree, the costs incurred by the females as a

result of mating with males having long tails (the decrease in growth and reproduction

in daughters).

Thus, by mating with males possessing proportionally long tails, female

guppies may not only incur costs but also obtain benefits, as mentioned earlier.

Further examination of the degree and influence of the costs and benefits of mating with

males having long tails on the lifetime fitness of females is required.   In addition, it is

still unclear why the body sizes of sons of the long-tailed males were not smaller than

those of the short-tailed males, whereas daughters of the former males were smaller

than those of the latter.   It is possible that, depending on tail lengths of their mates,

there is a difference in the parental investment, such as nutritional or hormonal

investment (Gil et al., 1999; Cunningham & Russell, 2000), made by females in their

sons and daughters.   Further studies will reveal the pattern of conflict between male

deception through tail elongation and female counter-adaptations in the guppy.

References

Abrahams, M.V. (1993). The trade-off between foraging and courting in male guppies.--

    Anim. Behav. 45: 673-681.

Andersson, M. (1994). Sexual selection.-- Princeton University Press, New Jersey.

Arnqvist, G. & Rowe, L. (2005). Sexual conflict.-- Princeton University Press, New

    Jersey.

Backwell, P.R.Y., Christy, J.H., Telford, S.R., Jennions, M.D. & Passmore, N.I. (2000).

    Dishonest signalling in a fiddler crab.-- Proc. R. Soc. Lond. B 267: 719-724.

Basolo, A.L. (1998). Shift in investment between sexually selected traits: tarnishing of

the silver spoon.-- Anim. Behav. 55: 665-671.

Bischoff, R.J., Gould, J.L. & Rubenstein, D.I. (1985). Tail size and female choice in the

guppy (Poecilia reticulata).-- Behav. Ecol. Sociobiol. 17: 253-255.

Brooks, R. & Caithness, N. (1995). Female choice in a feral guppy population: are there

multiple cues?-- Anim. Behav. 50: 301-307.

Brown, W.D., Crespi, B.J. & Choe, J.C. (1997). Sexual conflict and the evolution of

mating systems.   In: The evolution of mating systems in insects and arachnids

(J.C. Choe & B.J. Crespi, eds).-- Cambridge University Press, Cambridge, p. 352-

377.

Candolin, U. (1999). The relationship between signal quality and physical condition: is

sexual signalling honest in the three-spined stickleback?-- Anim. Behav. 58: 1261-

1267.

Chapman, T., Arnqvist, G., Bangham, J. & Rowe, L. (2003). Sexual conflict.-- Trends

Ecol. Evol. 18: 41-47.

Cunningham, E.J.A. & Russell, A.F. (2000). Egg investment is influenced by male

attractiveness in the mallard.-- Nature 404: 74-77.

Dawkins, M.S. & Guilford, T. (1991). The corruption of honest signalling.-- Anim.

Behav. 41: 865-873.

Eberhard, W.G. & Cordero, C. (2003) Sexual conflict and female choice.-- Trends Ecol.

Evol. 18: 438-439.

Endler, J.A. (1980). Natural selection on color patterns in Poecilia reticulata.--

Evolution 34: 76-91.

Gil, D., Graves, J., Hazon, N. & Wells, A. (1999). Male attractiveness and differential

testosterone investment in zebra finch eggs.-- Science 286: 126-128.

Houde, A.E. (1987). Mate choice based upon naturally occurring color pattern variation

in a guppy population.-- Evolution 41: 1-10.

Houde, A.E. (1997). Sex, color, and mate choice in guppies.-- Princeton University

Press, New Jersey.

Johnstone, R.A. (1997). The evolution of animal signals.-- In: Behavioural ecology, 4th

edn (J.R. Krebs & N.B. Davies, eds).-- Blackwell Science, Oxford, p. 155-178.

Johnstone, R.A. & Grafen, A. (1993). Dishonesty and the handicap principle.-- Anim.

Behav. 46: 759-764.

Karino, K. & Haijima, Y. (2001). Heritability of male secondary sexual traits in feral

   guppies in Japan.-- J. Ethol. 19: 33-37.

Karino, K. & Kobayashi, M. (2005). Male alternative mating behaviour depending on

   tail length of the guppy, Poecilia reticulata.-- Behaviour 142: 191-202.

Karino, K. & Matsunaga, J. (2002). Female mate preference is for male total length, not

   tail length in feral guppies.-- Behaviour 139: 1491-1508.

Kodric-Brown, A. (1989). Dietary carotenoids and male mating success in the guppy: an

   environmental component to female choice.-- Behav. Ecol. Sociobiol. 25: 393-401.

Kokko, H. (1997). Evolutionary stable strategies of age-dependent sexual

   advertisement.-- Behav. Ecol. Sociobiol. 41: 99-107.

Kokko, H., Brooks, R., Jennions, M.D. & Morley, J. (2003). The evolution of mate

   choice and mating biases.-- Proc. R. Soc. Lond. B 270: 653-664.

MacLaren, R.D., Rowland, W.J. & Morgan, N. (2004). Female preferences for sailfin

   and body size in the sailfin molly, Poecilia latipinna.-- Ethology 110: 363-379.

Maklakov, A.A., Blide, T. & Lubin, Y. (2005). Sexual conflict in the wild: elevated

   mating rate reduces female lifetime reproductive success.-- Am. Nat. 165: s38-s45.

Magurran, A.E. & Seghers, B.H. (1994). Sexual conflict as a consequence of ecology:

evidence from guppy, Poecilia reticulata, population in Trinidad.-- Proc. R. Soc.

Lond. B 255: 31-36.

Miller, K.B. (2003). The Phylogeny of diving beetles (Coleoptera: Dytiscidae) and the

evolution of sexual conflict.-- Biol. J. Linn. Soc. 79: 359-388.

Reynolds, J.D. & Gross, M.R. (1992). Female mate preference enhances offspring

growth and reproduction in a fish, Poecilia reticulata.-- Proc. R. Soc. Lond. B 250:

57-62.

Reznick, D.A., Bryga, H. & Endler, J.A. (1990). Experimentally induced life-history

evolution in a natural population.-- Nature 346: 357-359.

Rosenthal, G.G. & Evans, C. (1998). Female preference for swords in Xiphophorus

helleri reflects a bias for large apparent size.-- Proc. Natl. Acad. Sci. USA 95:

4431-4436.

Ryan, M.J. (1997). Sexual selection and mate choice.   In: Behavioural ecology, 4th edn

(J.R. Krebs & N.B. Davies, eds).-- Blackwell Science, Oxford, p. 179-202.

Weldon, P.J. & Burghardt, G.M. (1984). Deception divergence and sexual selection.-- Z.

Tierpsychol. 65: 89-102.

Zeh, J.A. & Zeh, D.W. (2003). Toward a new sexual selection paradigm: polyandry,

conflict and incompatibility.-- Ethology 109: 929-950.

Table 1.   Mean ± SE of morphological traits of parental (P) males and females.

Statistical analysis was conducted by paired t-test.

	Long-tailed	Short-tailed	t	p
P males (N = 20 pairs)				
Total length (mm)	21.6 ± 0.4	21.6 ± 0.4	0.2	0.83
Standard length (mm)	14.2 ± 0.3	16.5 ± 0.3	-17.1	< 0.001
Tail length (mm)	7.4 ± 0.2	5.0 ± 0.2	31.3	< 0.001
P females (N = 20 pairs)				
Total length (mm)	25.4 ± 0.7	25.1 ± 0.7	1.1	0.27
Standard length (mm)	18.8 ± 0.5	18.7 ± 0.4	0.3	0.78
Tail length (mm)	6.6 ± 0.3	6.4 ± 0.3	1.4	0.18

Table 2.   Mean ± SE of morphological traits of F1 males and females at 120 days after

their birth.   Statistical analysis was conducted by paired t-test.

	P males			
	Long-tailed	Short-tailed	t	p
F1 males (N = 20 pair broods; mean 4.3 ± 0.3 SE male offspring per P female)				
Total length (mm)	21.0 ± 0.4	20.0 ± 0.3	2.8	0.01
Standard length (mm)	14.7 ± 0.3	14.7 ± 0.3	-0.1	0.91
Tail length (mm)	6.2 ± 0.3	5.3 ± 0.2	3.2	0.005
F1 females (N = 20 pair broods; mean 4.5 ± 0.4 SE female offspring per P female)				
Total length (mm)	22.2 ± 0.6	24.0 ± 0.6	-3.5	0.003
Standard length (mm)	16.1 ± 0.5	17.6 ± 0.5	-3.1	0.006
Tail length (mm)	6.1 ± 0.3	6.4 ± 0.2	-1.8	0.08

Figure legends

Figure 1.   Comparisons of the number of F1 offspring (a) and the mean total length of

F1 offspring at 10 days after birth (b) between long-tailed P males and short-tailed P

males.   Means are given ± SE.

Figure 2.   Comparisons of the number of F2 offspring (a) and the mean total length of

F2 offspring at 10 days after birth (b) between those of descendants from long-tailed P

males and short-tailed P males.   Means are given ± SE.

Figure 3.   Relationships between (a) body sizes of F1 females and the number of F2

offspring and (b) body sizes of F1 females and the mean total lengths of F2 offspring at

10 days after birth.   Solid circles and the solid line indicate descendants of long-tailed

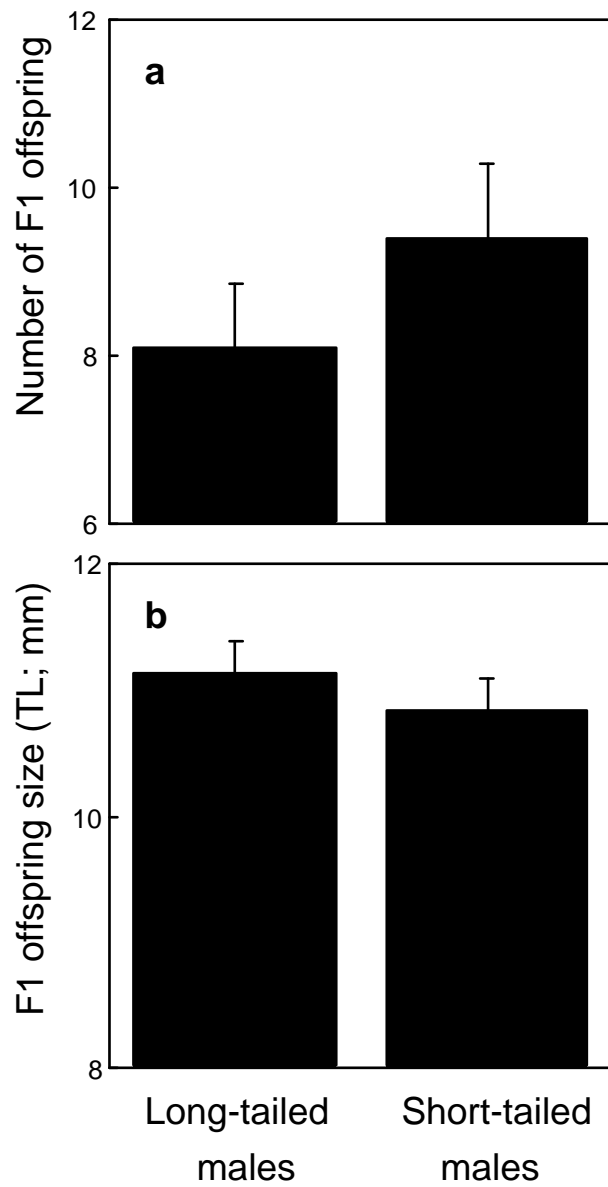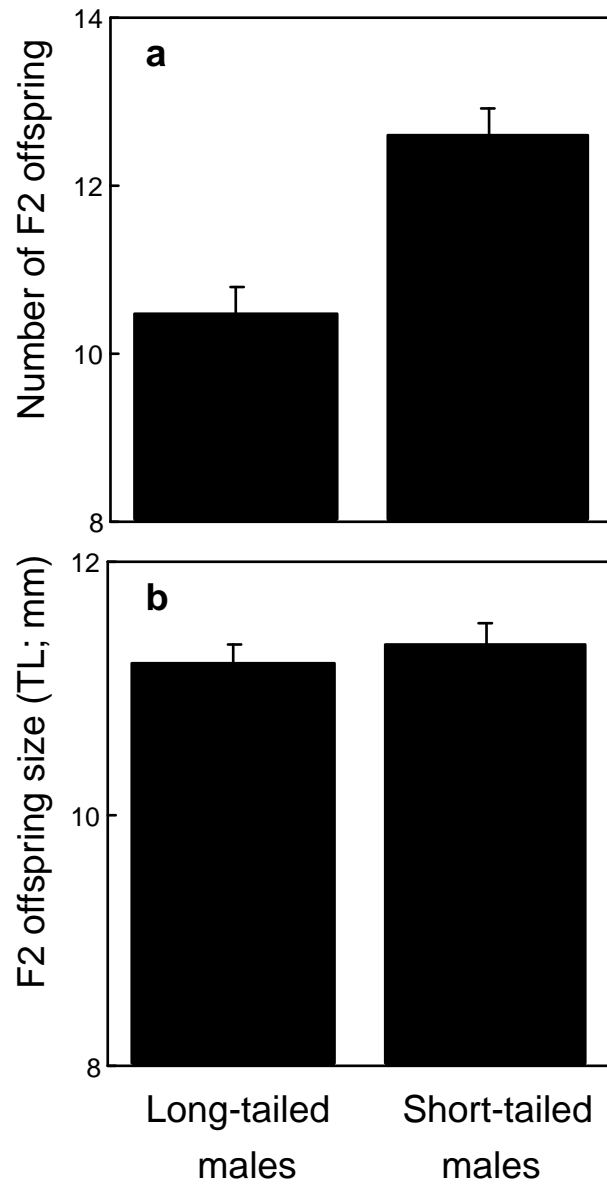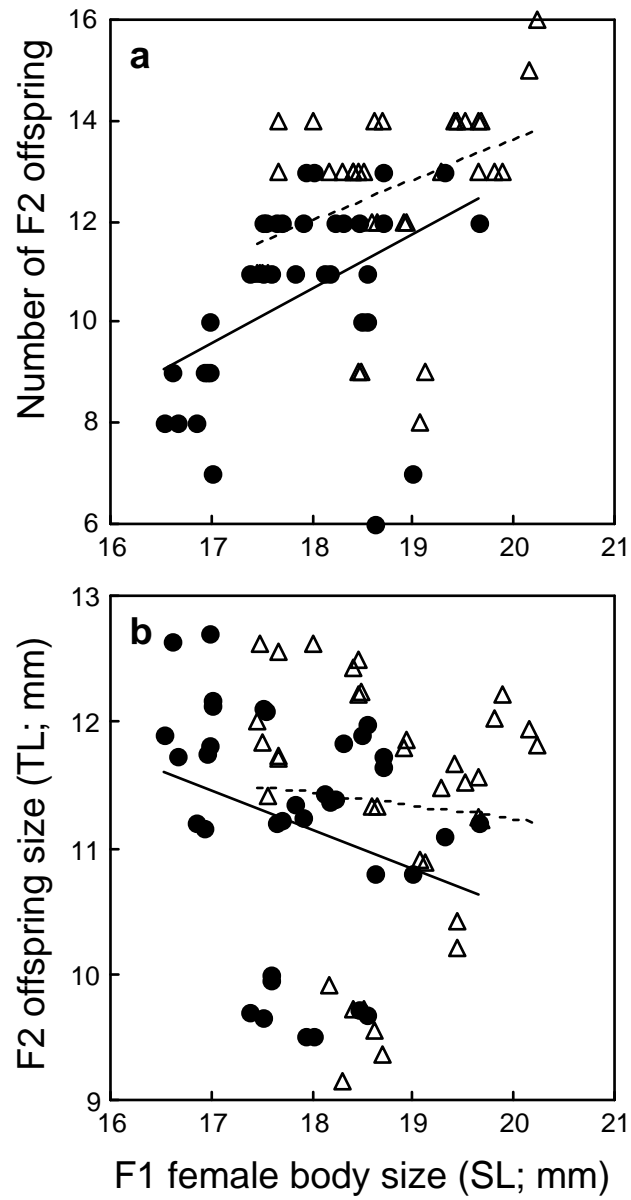P males, and open triangles and the broken line show those of short-tailed P males.

Figure 1. (Karino et al.)

Figure 2. (Karino et al.)

Figure 3. (Karino et al.)