

Unexpected offspring sex ratios in response to habitat quality in a size-dimorphic bark beetle

Risa D. Sargent and Mary L. Reid

Abstract: Facultative sex ratio manipulation has been examined in a limited number of diploid species, mainly vertebrates. We tested the prediction that mothers would preferentially place males in conditions conducive to large size in the diploid pine engraver bark beetle, *Ips pini*. In this species, males are the larger sex and therefore male reproductive success was expected to be more dependent on body size than female reproductive success. Because body size is largely environmentally determined in bark beetles, mothers were expected to alter sex ratios in response to habitat quality. Contrary to predictions, offspring sex ratios tended to be more female biased in situations conducive to large offspring size than in situations producing offspring of small size. We were able to rule out nonadaptive explanations such as differential mortality or development times of males and females, suggesting that the observed pattern is adaptive. This study provides a rare example of sex ratio manipulation in diploid insects. However, the unexpected direction of sex ratio biases suggests that daughters gain a yet unknown benefit from being reared in high-quality conditions that surpasses the fitness that would be gained from producing relatively larger sons.

Résumé : La manipulation facultative du rapport mâles : femelles a été étudiée chez un nombre restreint d'espèces diploïdes, surtout des vertébrés. Nous avons éprouvé l'hypothèse selon laquelle les mères ont probablement tendance à placer leurs rejetons mâles dans des conditions qui favorisent une grande taille chez le Scolyte du pin, *Ips pini*, un coléoptère diploïde. Chez cette espèce, les mâles sont plus gros que les femelles et, par conséquent, il faut s'attendre à ce que leur succès reproducteur repose davantage sur leur taille que celui des femelles. Comme la taille est en grande partie fonction du milieu chez les scolytes, les mères modifient sans doute la proportion de mâles et de femelles de leur progéniture en réponse à la qualité de l'habitat. Contrairement aux prédictions, le rapport mâles : femelles chez les rejetons a plus tendance à avantager les femelles dans les situations favorisant une grande taille que dans les situations favorisant une petite taille. Nous avons été en mesure d'éliminer les facteurs explicatifs ne reposant pas sur l'adaptation, comme la mortalité ou la durée du développement, différentes chez les mâles et les femelles, ce qui semble indiquer que les résultats observés relèvent de facteurs d'adaptation. Cette étude expose un exemple inusité de manipulation du rapport mâles : femelles chez des insectes diploïdes. Cependant, le rapport mâles : femelles inattendu semble indiquer que les rejetons filles tirent un bénéfice encore indéterminé de l'élevage dans des conditions de haute qualité, bénéfice qui dépasse le fitness qui serait obtenu à la production de rejetons mâles de taille relativement grande.

[Traduit par la Rédaction]

Introduction

Sex ratio manipulation can evolve when the fitness of one sex is more dependent on resource allocation than is the fitness of the other sex (Trivers and Willard 1973; Charnov 1982; Clutton-Brock et al. 1984; Frank 1990). Trivers and Willard (1973) reasoned that in harem polygynous species, male reproductive success is more dependent on maternal condition than is female reproductive success. Thus, mothers in good condition should skew their sex ratio towards males. This prediction has been supported in several studies of vertebrates (Clutton-Brock and Iason 1986). However, there is increasing concern that published studies are biased towards favourable results and that adaptive sex ratio manipulation

may not be as widespread as it appears to be in the literature (Clutton-Brock and Iason 1986; Green and Berger 1990; Festa-Bianchet 1996). In addition, several studies have reported sex ratio patterns opposite to that predicted by the Trivers and Willard (1973) hypothesis (e.g., Silk 1983; Verme 1983). Thus, the extent to which the Trivers and Willard hypothesis explains sex ratios in nature remains unclear.

In most insect species, females are assumed to benefit relatively more from large size than males (Thornhill and Alcock 1983; Honěk 1993; Strohm and Linsenmair 1997) because of the positive correlation between female fecundity and body size (Honěk 1993). Hence, selection generally operates to increase female body size in insects, resulting in a sexual dimorphism with females being larger than males (Ghiselin 1974).

One exception to this pattern of size dimorphism in insects is the bark beetle genus *Ips* (Coleoptera: Scolytidae), a harem polygynous group where average male size generally exceeds average female size (Wood and Stark 1968; Garraway 1986; Haack et al. 1987a; Reid and Roitberg 1995). In this genus, males initiate breeding sites (nuptial chambers) to which females are attracted. There are several reasons why selection might act to increase male size over female size in *Ips* species. Males suffer a higher mortality

Received June 4, 1998. Accepted January 8, 1999.

R.D. Sargent¹ and M.L. Reid. Kananaskis Field Stations and Department of Biological Sciences, University of Calgary, Calgary, AB T2N 1N4, Canada.

¹Author to whom all correspondence should be sent. Present address: Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada (e-mail: rdsargent@sfu.ca).

ty risk than females when searching for suitable mating grounds (Cook et al. 1983) and this mortality risk may be lower for large individuals (Safranyik 1976; Anderbrant 1988; Robertson and Roitberg 1998). Large males also have better dispersal abilities (Robertson and Roitberg 1998) and produce more pheromones than do small males (Anderbrant et al. 1985; Conner et al. 1990). Large males produce more offspring per brood in spite of deserting their broods earlier than small males (Reid and Roitberg 1995; Robertson 1998) and females prefer to mate with larger males (Robertson 1998; M. Reid, in preparation). Thus, *Ips* males may benefit considerably from a larger size in terms of lower mortality, better dispersal ability, and higher reproductive success.

In bark beetles, intraspecific variation in body size is primarily the result of variation in the larval environment, especially brood density and phloem quality (Haack et al. 1987a; Anderbrant and Schlyter 1989). Progeny reared in low densities or thick phloem tend to be larger, have larger fat reserves, and can therefore fly farther than those reared in high densities or thin phloem (Anderbrant 1988). Rearing conditions may also vary within a single female's brood; bark beetles lay their eggs sequentially along egg galleries and later laid offspring experience greater phloem deterioration and higher competition than early laid offspring (Beaver 1974). Thus, offspring emerging from late gallery positions tend to be smaller than those emerging from early gallery positions (Beaver 1974).

The purpose of this study is to examine the effects of habitat quality and gallery position on body size and sex ratios in pine engravers, *Ips pini*. Pine engravers breed primarily in the phloems of freshly dead pines across North America. Each male establishes a nuptial chamber and typically attracts three mates (Swaby and Rudinsky 1976; Reid and Roitberg 1994). Males remain with their mates and brood during oviposition, during which time they provide paternal care (Reid and Roitberg 1994; Robertson 1998) and mate repeatedly (Schmitz 1972; Lissemore 1997; M. Reid, personal observation). Breeding sites generally support only a single generation so that individuals must fly in search of new breeding sites before each breeding bout. As in other *Ips* species, body size may vary in response to brood habitat quality such as breeding density, but males are consistently larger than females that are produced under the same conditions (Anderbrant et al. 1985; Rankin and Borden 1991; Robins and Reid 1997). Based on the mating system and size dimorphism of pine engravers and the effects of habitat quality on body size, we predicted that males would be preferentially placed in habitats with a better phloem and in early gallery positions.

Methods

We tested our hypothesis using two approaches. First, we examined sex ratios among broods and over the emergence period in relation to body size through the collection of naturally emerging pine engravers. Second, we examined sex ratio as a function of offspring position in the egg gallery through the artificial rearing of eggs from known gallery positions.

Emergence experiment

Ten 30 cm long experimental logs were obtained from each of two arbitrarily chosen uninfested lodgepole pine trees, *Pinus*

contorta, ca. 110 and 80 years of age. Log diameter and width of the last 5 years' growth rings were measured as indices of tree quality and phloem thickness (Cole 1973). All experimental rearing was done in logs or phloems taken from lodgepole pine trees.

Parental pine engravers were collected upon emergence from trees that had been naturally colonized. Sex was determined by examining elytral spine length (Lanier and Cameron 1969). To establish egg galleries, males were randomly assigned to logs and confined within vials placed over small holes punched through the bark midway up the log. As soon as nuptial chamber construction was detected (approximately 24 h after male introduction), a randomly assigned female was introduced to each vial. If a male did not construct a nuptial chamber within 48 h, he was replaced, and if a female did not enter the nuptial chamber within 48 h, she was replaced. Prior to introduction, parental body size was measured as pronotum width to the nearest 0.02 mm using a microscope fitted with an ocular micrometer.

Once gallery construction was initiated, the 20 logs were randomly assigned to individual cages. Cages were kept on shelves in a temperature-controlled laboratory at the University of Calgary (20–24°C, 20–25% relative humidity). Each cage had a translucent funnel attached to the base to which a collection vial was attached. Lights were placed under the cages to ensure that emerging beetles would be attracted promptly to the collection vials. The lights were on a timer providing 12 h of light per day. Emergent beetles were collected daily and their pronotum width and sex were determined. The first emergent male and female with similar widths to the parents were omitted from the analyses to ensure that only offspring were used. For half of the logs in each tree-quality category ($n = 10$ logs total), we excavated the galleries after the first few offspring had emerged to assess the actual position in the gallery of each offspring. However, we found that the offspring had burrowed too far from the egg gallery for us to be certain of their original position. These logs still provided brood size and sex ratio data. The remaining logs were left undisturbed so that continued emergence data could be collected. These logs were used to examine how body size and sex ratio varied with respect to emergence time. All data were examined for normality and transformed as required.

Rearing experiment

We also examined sex ratio as a function of actual position in the gallery by collecting offspring prior to emergence and rearing them to adulthood in an artificial medium for sexing.

Parental pine engravers were collected from a laboratory population that originated from naturally attacked lodgepole pine trees. For this experiment all 20 logs were from the same recently felled tree, ca. 90 years of age. Methods for parental introduction were identical to the previous experiment except that twice as many galleries were initiated by introducing two males on opposite sides of each log. Gallery construction was allowed to progress until test log peels demonstrated that eggs were no longer being oviposited. Oviposition order and distance from the beginning of the gallery were recorded for each offspring.

Phloem-medium preparation and rearing methods followed Whitney and Spanier (1982). Briefly, this involved placing eggs or larvae in individual vials with a medium of ground phloem and brewer's yeast and incubating them. Once adult beetles were observed in the medium (or fungal growth prevented beetle survival), beetles were removed and their sex was determined.

Data are presented as the mean \pm SE.

Results

Emergence experiment

Of the twenty broods that were initiated, six failed to produce offspring, three from each tree. The mean number of offspring emerging from a successful brood was 9.86 ± 1.49

Table 1. Offspring characteristics in good- and poor-quality phloem.

	Good-quality logs	Poor-quality logs	<i>F</i>	<i>p</i>
Brood size ^a	12.2±1.83 (7)	12.2±1.83 (7)	0.00	1.00
Sex ratio ^b	0.33±0.044 (7)	0.65±0.055 (7)	21.7	0.0035
Emergence time (days) ^c	40.0±1.01 (51)	63.4±2.95 (24)	19.5	<0.0001
Offspring size (mm) ^a	1.48±0.009 (68)	1.45±0.008 (70)	5.56	0.002

Note: Values are given as the mean ± SE. Numbers in parentheses are sample sizes.

^aLeast squares means; controlling for brood origin.

^bProportion male; controlling for brood size.

^cTime since initiation of gallery by parental female.

($n = 14$). Male offspring from a given brood were significantly larger than female offspring (male pronotum width = 1.48 ± 0.008 mm, $n = 57$; female pronotum width = 1.44 ± 0.009 mm, $n = 75$; sex effect: $F = 14.5$, $df = 1,117$, $p = 0.0002$; brood effect: $F = 6.68$, $df = 13,117$, $p < 0.0001$). The mean body size of males and females within broods were highly correlated ($r = 0.913$, $df = 1,11$, $p < 0.0001$). The mean brood sex ratio was 0.527 ± 0.066 proportion male ($n = 14$), not significantly different from 0.5 ($t = 0.412$, $df = 13$, $p > 0.5$).

We used mean offspring body size and mean brood size as measures of habitat quality. Brood size is defined as the number of adults emerging from a clutch. Because of the importance of environmental conditions on body size and brood size in bark beetles, these measures can be used as an indication of rearing conditions. These two variables were positively correlated ($r = 0.581$, $df = 1,12$, $p = 0.029$), and therefore we examined their effects on sex ratio separately. In each of these analyses we also included tree quality (see below). The proportion of males in a brood decreased significantly with increasing mean offspring size (Fig. 1a: $F = 17.1$, $df = 2,11$, $p = 0.002$) and with increasing brood size (Fig. 1b: $F = 5.58$, $df = 2,11$, $p = 0.0018$), contrary to our prediction. In fact, the two largest broods ($n = 19$, 18) were very strongly female biased, with sex ratios differing significantly from 50% ($\chi^2 = 8.90$, $df = 1$, $p < 0.003$ and $\chi^2 = 17.23$, $df = 1$, $p < 0.0001$).

In addition to the effects of mean body size and brood size, there was an effect of tree identity on brood sex ratio (Fig. 1a: $F = 11.1$, $df = 1,11$, $p = 0.007$; Fig. 1b: $F = 4.99$, $df = 1,11$, $p = 0.0473$). Tree quality can be defined a priori on the basis of recent growth rate and size (Cole 1973). The trees differed significantly in these indices of the tree quality (tree 1: mean diameter = 18.25 ± 0.55 cm, tree 2 = 12.05 ± 0.55 cm, $t = 8.02$, $df = 18$, $p < 0.0001$; tree 1: mean width of last five rings = 3.19 ± 0.44 mm, tree 2 = 0.50 ± 0.57 mm, $t = 3.8$, $df = 6$, $p = 0.010$). The tree with the largest diameter and width of last five rings (tree 1) will hereafter be referred to as the good-quality tree (Cole 1973). There was no difference in the number of offspring emerging from logs from the two trees (Table 1). However, offspring reared in the good-quality tree emerged significantly earlier and were significantly wider than beetles emerging from the other tree (Table 1). Contrary to expectation, the brood sex ratio of offspring reared in good-quality logs was significantly more female biased than the brood sex ratio of offspring reared in poor-quality logs (Table 1; Figs. 1a and 1b).

We also examined how body size and sex ratio varied over the emergence period and whether body size and sex ratio varied with emergence date within individual broods

(cages). Pronotal width was tested as a function of date (ln transformed), cage (nested within tree quality), tree quality, and sex. The relationship between offspring size and emergence time depended on tree quality (ANCOVA quality \times time interaction: $F = 4.33$, $df = 1,61$, $p = 0.0416$). In good-quality logs, offspring size declined significantly over time ($F = 4.44$, $df = 6,43$, $p = 0.0410$). In poor-quality logs, there was no significant relationship between size and date of emergence ($F = 1.39$, $df = 6,17$, $p = 0.255$). In each of these models, there was also a significant effect of cage (poor: $F = 3.78$, $df = 4,17$, $p = 0.0224$; good: $F = 7.16$, $df = 4,43$, $p = 0.0002$), and in good-quality logs an effect of sex ($F = 15.4$, $df = 1,43$, $p = 0.0003$).

Sex ratio was similarly examined as a function of date (ln transformed), cage, and tree quality. Here there was no effect of cage ($\chi^2 = 3.48$, $df = 8$, $p = 0.901$) or tree quality ($\chi^2 = 0.362$, $df = 1$, $p = 0.548$). Again contrary to the expectation that males would be oviposited first, the probability of an offspring being male increased with date of emergence (Fig. 2: logistic regression, $\chi^2 = 13.9$, $df = 1$, $p < 0.0002$). The 95% confidence interval for female emergence was 38.5–42.3 days to emergence ($n = 44$), while it was 53.2–59.5 days for males ($n = 31$, $t = 4.54$, $p < 0.0001$).

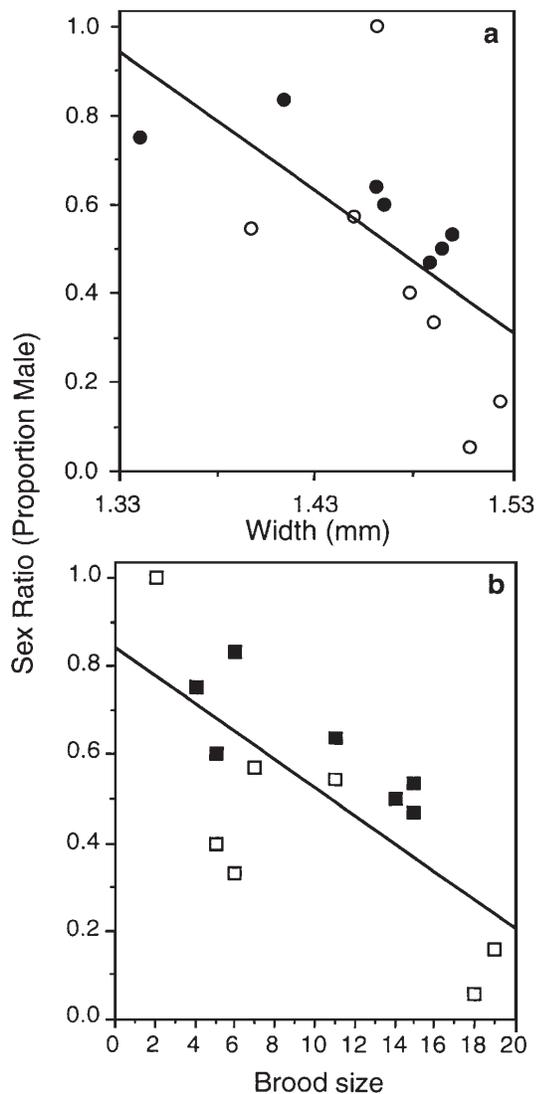
The relationship between emergence date and offspring sex within broods did not differ significantly between the two log qualities (interaction: $\chi^2 = 1.50$, $df = 1$, $p = 0.222$). However, because good- and poor-quality logs produced different relationships between offspring size and date of emergence, we also examined the relationship between sex and emergence date for the two log qualities separately. In good-quality logs, the probability that an offspring was male increased with date of emergence ($\chi^2 = 10.5$, $df = 1$, $p = 0.0012$), but there was no such relationship in poor-quality logs ($\chi^2 = 0.874$, $df = 1$, $p = 0.345$). Thus, effects of emergence time on sex ratio were consistent with effects of emergence time on body size.

Rearing experiment

The rearing experiment was performed to ensure that emergence time reflected actual beetle position and was not an artifact of differential development rates between the sexes. The pattern of results for the rearing experiment was very similar to those of the emergence experiment. The mean number of offspring surviving from each brood was 9.22 ± 1.01 ($n = 28$). The average brood sex ratio was 0.475 ± 0.051 proportion males, not significantly different from 0.5 ($t = -0.500$, $df = 27$, $p > 0.5$).

Consistent with the results of the emergence experiment, mean male offspring distance from the nuptial chamber (45.8 ± 3.5 mm) was significantly greater than mean female

Fig. 1. The relationship between brood sex ratio and (a) mean offspring size in poor-quality (●) and good-quality (○) logs ($y = 5.09 - 3.12x$, $p = 0.002$) and (b) brood size in poor-quality (■) and good-quality (□) logs ($y = 0.839 - 0.0316x$).

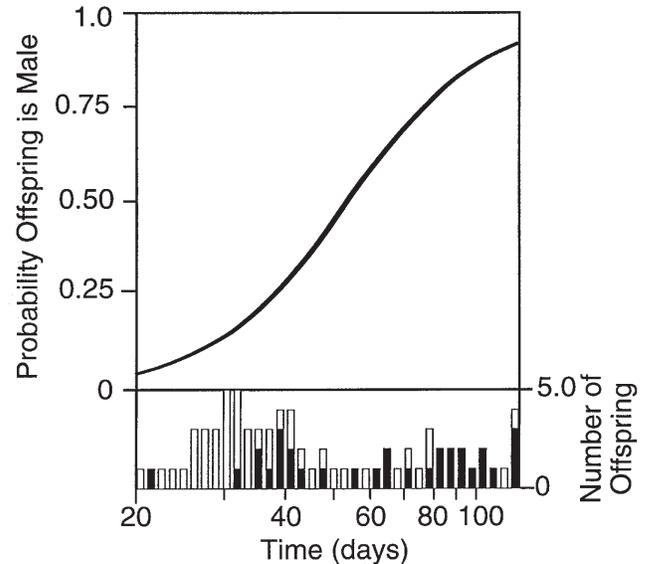


offspring distance ($33.9 \pm 2.3\text{mm}$; paired t test: $t = 1.71$, $df = 27$, $p = 0.05$). Thus the probability of an offspring being male increased with distance from the nuptial chamber (logistic regression model: $\chi^2 = 8.37$, $df = 1$, $p = 0.0038$). This relationship did not differ among broods ($\chi^2 = 8.37$, $df = 21$, $p = 0.960$). The sex ratio of the first two offspring in each brood was significantly female biased (62.0% females, $\chi^2 = 4.11$, $df = 1$, $p = 0.0426$).

Discussion

We expected that male pine engravers would benefit most from habitats favouring large offspring body size because males are the larger sex under most conditions (Wagner et al. 1987; Rankin and Borden 1991; Teale et al. 1994; Robins and Reid 1997). However, males were more likely to be produced in habitats producing smaller individuals. Sex ratios were consistently male biased in broods with smaller mean offspring body size, in poor-quality relative to good-quality

Fig. 2. Logistic regression on the relationship between offspring sex and emergence time (days) after gallery initiation ($p = 1 / (1 + \exp [-12.6 + 3.19x])$). The frequency distribution indicates the proportion of emerging beetles that are female (open) and male (shaded) on each day.



logs, and in the later egg positions within a gallery. An increase in the proportion of males as emergence continues has also been observed in other *Ips* species (Wagner et al. 1987, 1988).

Although primary sex ratios were not measured in this study, it is unlikely that postoviposition processes can explain our results. One common explanation for biased sex ratios in bark beetles is that the sexes experience differential mortality in response to stress (e.g., Safranyik 1976; Flamm et al. 1987; Haack et al. 1987a, 1987b; Kirkendall 1993), although this has never been demonstrated directly. In our study, two results refute differential mortality. First, brood sizes were similar in the two log qualities, but sex ratios were not. Second, sex ratios tended to be female biased in good conditions, not equal, such as in large broods and in the first gallery positions. It is unlikely that males would have high mortality in good conditions but low mortality in poor conditions.

Another possible explanation for the earlier emergence of one sex is that development time is less for that sex, although this has not been detected despite detailed studies of development in two *Ips* species (Wagner et al. 1987, 1988). In the present study, this explanation is unlikely because gallery excavations revealed that emergent sex ratio patterns were consistent with actual gallery position. Moreover, differential development does not explain the sex ratio differences among broods from different log qualities. Therefore we conclude that the observed sex ratio patterns are due to parental manipulation of sex ratio.

Facultative sex ratio manipulation is most commonly observed in haplodiploid insects, rarely in diploid insects (McLain and Marsh 1990). Pine engravers are diploid with a heterogametic sex-determining mechanism (Lanier 1966), and the mechanism by which mothers could manipulate sex ratio is unknown. In another bark beetle, *Dendroctonus*

ponderosae, some fertilized eggs are passed to the bursa copulatrix where they are ruptured rather than being laid (Cerezke 1964). If the same mechanism is present in pine engravers, it could allow females to manipulate offspring sex.

If females are manipulating offspring sex ratio to increase their fitness, daughters must receive some benefit from good habitat quality that exceeds the large size advantage that males would obtain from being reared in better quality habitats. The nature of such a benefit is difficult to assess especially given the pre-eminence of body size as a fitness determinant (Thornhill and Alcock 1983). One possibility is that female pine engravers benefit more from early emergence that is associated with being placed in early gallery positions and in good-quality logs. It is possible that small female size is a by-product of selection for early emergence (Andersson 1994), although size does not necessarily correlate with development time (Klingenberg and Spence 1997). Females that emerge early might have a better chance of joining an unmated male rather than a harem, which could have significant fitness advantages (Kirkendall 1989), but this potential advantage depends critically on the timing of an individual's breeding bout with respect to the phenology of breeding in the population.

Another proposed benefit of females emerging before males is inbreeding avoidance (Cameron and Borden 1967). However, there are several difficulties with this hypothesis. First, thousands of pine engravers emerge from a typical breeding site, making it unlikely that a sister would encounter her brother. Second, in *D. ponderosae* (a bark beetle species in which females initiate breeding sites and males follow) females are more likely to be placed in earlier gallery positions (data extracted from Amman and Bartos 1991). Finally, the inbreeding hypothesis does not explain between-brood differences in sex ratio.

It is also possible that female pine engravers require some trace nutrient that is more likely to be found in the phloem of trees with a high growth rate and in nondeteriorated phloem found at the beginning of egg galleries. For example, it has been suggested that females receive different amounts of phosphorus from thick phloem and thin phloem (Popp et al. 1989). Such a nutrient might be important in a female function such as egg formation. Males, on the other hand, may obtain the large size that enhances their fitness due to carbohydrates that are less ephemeral than the postulated trace nutrient. To test this hypothesis, we need to identify the nutrient(s) involved and then determine whether its impact on female fitness exceeds the impact of body size on male fitness.

This study began with a hypothesis founded on established theory pertaining to sex ratio manipulation in pine engravers based on their mating system and sexual dimorphism. We found that although offspring size was related to phloem quality in the predicted manner, the sex ratio pattern was opposite to our prediction. We were able to rule out nonadaptive explanations such as differential mortality and development, suggesting that the observed pattern is adaptive. To our knowledge, this is only the third example of sex ratio manipulation in a diploid insect (McLain and Marsh 1990; Reinhold 1996). However, this study challenges the

assumption that body size dimorphism reflects sexual differences in fitness returns with investment (Stamps 1990) and highlights the need for further tests of the Trivers and Willard (1973) hypothesis.

Acknowledgements

We thank G. Robins for assistance with data collection, J. Buchanan-Mappin (Kananaskis Field Stations) for providing supplies and equipment, and T. Hindmarch for supplying beetles. S. Frank, R. Lalonde, E. Mondor, I. Robertson, K. Webster, three anonymous reviewers, and the Sex Papers: Evening Review Meetings discussion group at Kananaskis Field Stations provided helpful comments on the manuscript. This study was supported by a Natural Sciences and Engineering Research Council of Canada research grant to M.L.R.

References

- Amman, G.D., and Bartos, D.L. 1991. Mountain pine beetle offspring characteristics associated with females producing first and second broods, male presence and egg gallery length. *Environ. Entomol.* **20**: 1562–1567.
- Anderbrant, O. 1988. Survival of parent and brood adult bark beetles, *Ips typographus*, in relation to size, lipid content, and re-emergence or emergence day. *Physiol. Entomol.* **13**: 121–129.
- Anderbrant, O., and Schlyter, F. 1989. Causes and effect of individual quality in bark beetles. *Holarct. Ecol.* **12**: 488–493.
- Anderbrant, O., Schlyter, F., and Birgersson, G. 1985. Intraspecific competition affecting parents and offspring in the bark beetle *Ips typographus*. *Oikos*, **45**: 89–98.
- Andersson, M. 1994. *Sexual selection*. Princeton University Press, Princeton, N.J.
- Beaver, R.A. 1974. Intraspecific competition among bark beetle larvae (Coleoptera: Scolytidae). *J. Anim. Ecol.* **43**: 455–467.
- Cameron, E.A., and Borden, J.H. 1967. Emergence patterns of *Ips confusus* (Coleoptera: Scolytidae) from ponderosa pine. *Can. Entomol.* **99**: 236–244.
- Cerezke, H.F. 1964. The morphology and functions of the reproductive systems of *Dendroctonus monticolae* Hopk. (Coleoptera: Scolytidae). *Can. Entomol.* **96**: 477–500.
- Charnov, E.L. 1982. *The theory of sex allocation*. Princeton University Press, Princeton, N.J.
- Clutton-Brock, T.H., and Iason, G.R. 1986. Sex ratio variation in mammals. *Q. Rev. Biol.* **61**: 339–374.
- Clutton-Brock, T.H., Albon, S.D., and Guinness, F.E. 1984. Maternal dominance, breeding success, and birth sex ratios in red deer. *Nature (Lond.)*, **308**: 358–360.
- Cole, D.M. 1973. Estimation of phloem thickness in lodgepole pine. USDA For. Serv. Res. Pap. INT-148.
- Conner, W.E., Roach, B., Benedict, E., Meinwald, J., and Eisner, T. 1990. Courtship pheromone production and body size as correlates of larval diet in males of the arctiid moth, *Utetheisa ornatrix*. *J. Chem. Ecol.* **16**: 543–552.
- Cook, S.P., Wagner, T.L., Flamm, R.O., Dickens, J.C., and Coulson, R.N. 1983. Examination of sex ratios and mating habits of *Ips avulsus* and *I. calligraphus* (Coleoptera: Scolytidae). *Ann. Entomol. Soc. Am.* **76**: 56–60.
- Festa-Bianchet, M. 1996. Offspring sex ratio studies of mammals: does publication depend upon the quality of the research or the direction of the results? *Ecoscience*, **3**: 42–44.

- Flamm, R.O., Cook, S.P., Wagner, T.L., Pulley, P.E., and Coulson, R.N. 1987. Reemergence and emergence of *Ips avulsus* and *Ips calligraphus* (Coleoptera: Scolytidae). *Environ. Entomol.* **16**: 869–876.
- Frank, S.A. 1990. Sex allocation theory for birds and mammals. *Annu. Rev. Ecol. Syst.* **21**: 13–55.
- Garraway, E. 1986. The biology of *Ips calligraphus* and *Ips grandicollis* (Coleoptera: Scolytidae) in Jamaica. *Can. Entomol.* **118**: 113–121.
- Ghiselin, M.T. 1974. The economy of nature and the evolution of sex. University of California Press, Berkeley.
- Green, W.C., and Berger, J. 1990. Maternal investment in sons and daughters: problems of methodology. *Behav. Ecol. Sociobiol.* **27**: 99–102.
- Haack, R.A., Wilkinson, R.C., and Foltz, J.L. 1987a. Plasticity in life-history traits of the bark beetle *Ips calligraphus* as influenced by bark thickness. *Oecologia*, **72**: 32–38.
- Haack, R.A., Wilkinson, R.C., Foltz, J.L., and Corneil, J.A. 1987b. Spatial attack pattern, reproduction, and brood development of *Ips calligraphus* (Coleoptera: Scolytidae) in relation to slash pine thickness: a field study. *Environ. Entomol.* **16**: 28–436.
- Honěk, A. 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos*, **66**: 483–492.
- Kirkendall, L.R. 1989. Within-harem competition among *Ips* females, an overlooked component of density-dependent larval mortality. *Holarct. Ecol.* **12**: 477–487.
- Kirkendall, L.R. 1993. Ecology and evolution of biased sex ratios in bark and ambrosia beetles. In *Evolution and diversity of sex ratio in insects and mites*. Edited by D. Wrensch and M. Ebbert. Chapman and Hall, New York. pp. 235–316.
- Klingenberg, C.P., and Spence, J.R. 1997. On the role of body size for life-history evolution. *Ecol. Entomol.* **22**: 55–68.
- Lanier, G.N. 1966. Interspecific mating and cytological studies of closely related species of *Ips* DeGeer and *Orthotomicus* Ferrari (Coleoptera: Scolytidae). *Can. Entomol.* **98**: 175–188.
- Lanier, G.N., and Cameron, A. 1969. Secondary sexual characteristics in the North American species of the genus *Ips* (Coleoptera: Scolytidae). *Can. Entomol.* **101**: 862–870.
- Lissemore, F.M. 1997. Frass-clearing by male pine engraver beetles (*Ips pini*; Scolytidae): paternal care or a novel form of paternity assurance? *Behav. Ecol.* **8**: 318–325.
- McLain, D.K., and Marsh, N.B. 1990. Individual sex ratio adjustment in response to the operational sex ratio in the southern green stinkbug. *Evolution*, **44**: 1018–1025.
- Popp, M.P., Wilkinson, R.C., Jokela, E.J., Harding, R.B., and Phillips, T.W. 1989. Effects of slash pine phloem on the reproductive performance of *Ips calligraphus* (Coleoptera: Scolytidae). *Environ. Entomol.* **18**: 795–799.
- Rankin, L.J., and Borden, J.H. 1991. Competitive interactions between the mountain pine beetle and the pine engraver in lodgepole pine. *Can. J. For. Res.* **21**: 1029–1036.
- Reid, M.L., and Roitberg, B.D. 1994. Benefits of prolonged residence with mates and brood in a bark beetle (Coleoptera: Scolytidae). *Oikos*, **70**: 140–148.
- Reid, M.L., and Roitberg, B.D. 1995. Effects of body size on investment in individual broods by male pine engravers (Coleoptera: Scolytidae). *Can. J. Zool.* **73**: 1396–1401.
- Reinhold, K. 1996. Biased primary sex ratio in the bushcricket *Poecilimon veluchianus*, an insect with sex chromosomes. *Behav. Ecol. Sociobiol.* **39**: 189–194.
- Robertson, I.C. 1998. Paternal care enhances male reproductive success in pine engraver beetles. *Anim. Behav.* **56**: 595–602.
- Robertson, I.C., and Roitberg, B.D. 1998. Duration of paternal care in pine engraver beetles: why do larger males care less? *Behav. Ecol. Sociobiol.* **43**: 379–386.
- Robins, G.L., and Reid, M.L. 1997. Effects of density on the reproductive success of pine engravers: is aggregation in dead trees beneficial? *Ecol. Entomol.* **22**: 329–334.
- Safranyik, L. 1976. Size and sex related emergence, and survival in cold storage, of mountain pine beetle adults. *Can. Entomol.* **108**: 209–212.
- Schmitz, R.F. 1972. Behavior of *Ips pini* during mating, oviposition, and larval development (Coleoptera: Scolytidae). *Can. Entomol.* **104**: 1723–1728.
- Silk, J.B. 1983. Local resource competition and facultative adjustment of sex ratios in relation to competitive activities. *Am. Nat.* **130**: 56–66.
- Stamps, J.A. 1990. When should avian parents differentially provision sons and daughters? *Am. Nat.* **135**: 671–685.
- Strohm, E., and Linsenmair, K.E. 1997. Low resource availability causes extremely male-biased investment ratios in the European beewolf, *Philanthus triangulum* F. (Hymenoptera, Sphecidae). *Proc. R. Soc. Lond. Ser. B Biol. Sci.* **264**: 423–429.
- Swaby, J.A., and Rudinsky, J.A. 1976. Acoustic and olfactory behaviour of *Ips pini* (Say) (Coleoptera: Scolytidae) during host invasion and colonisation. *Z. Angew. Entomol.* **81**: 421–432.
- Teale, S.A., Hager, B.J., and Webster, F.X. 1994. Pheromone-based assortative mating in a bark beetle. *Anim. Behav.* **48**: 569–578.
- Thornhill, R., and Alcock, J. 1983. The evolution of insect mating systems. Harvard University Press, Cambridge.
- Trivers, R.L., and Willard, D.F. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science* (Washington, D.C.), **179**: 90–92.
- Verme, L.J. 1983. Sex ratio variation in *Odocoileus*: a critical review. *J. Wildl. Manage.* **45**: 710–715.
- Wagner, T.L., Fargo, W.S., Flamm, R.O., Coulson, R.N., and Pulley, P.E. 1987. Development and mortality of *Ips calligraphus* (Coleoptera: Scolytidae) at constant temperatures. *Environ. Entomol.* **16**: 484–496.
- Wagner, T.L., Hennier, P.B., Flamm, R.O., and Coulson, R.N. 1988. Development and mortality of *Ips avulsus* (Coleoptera: Scolytidae) at constant temperatures. *Environ. Entomol.* **17**: 181–191.
- Whitney, H.S., and Spanier, O.J. 1982. An improved method for rearing axenic mountain pine beetles, *Dendroctonus ponderosae* (Coleoptera: Scolytidae). *Can. Entomol.* **114**: 1095–1100.
- Wood, D.L., and Stark, R.W. 1968. The life history of *Ips calligraphus* (Coleoptera: Scolytidae) with notes on its biology in California. *Can. Entomol.* **100**: 145–151.