ORIGINAL ARTICLE

Foraging ability in the scorpionfly *Panorpa vulgaris*: individual differences and heritability

M. Missoweit · S. Engels · K. P. Sauer

Abstract According to indicator models of sexual selection, mates may obtain indirect, i.e. genetic, benefits from choosing partners indicating high overall genetic quality by honest signals. In the scorpionfly *Panorpa vulgaris*, both sexes show mating preferences on the basis of the condition of the potential partners. Females prefer males that produce nuptial gifts (i.e. salivary secretions) during copulation, while males invest more nuptial gifts in females of high nutritional status. Both characters, males' ability to produce nuptial gifts and high nutritional status of females, are known to be reliable indicators of foraging ability. Thus, besides possible direct benefits, both sexes might also obtain indirect benefits in terms of "good foraging genes" by their choice and thereby increase the fitness of their offspring. A prerequisite for this possibility is the heritability of the respective trait. In the present study, we estimated the repeatability and the heritability of foraging ability. Our results indicate (1) a significant repeatability of individual foraging efficiencies in males and females and (2) a heritable component of this trait by a significant parent–offspring regression. These findings suggest that genetic benefits in terms of increased offspring foraging ability might contribute to selection for mating preferences in both sexes.

Keywords Heritability · Foraging ability · Indirect benefits · Sexual selection · Scorpionflies

M. Missoweit (✉) · S. Engels · K. P. Sauer
Institute for Evolutionary Biology and Ecology,
University of Bonn,
An der Immenburg 1,
53121 Bonn, Germany
e-mail: mmissoweit@evolution.uni-bonn.de

Introduction

Sexual selection theory proposes a direct and/or indirect increase of reproductive success by mate choice (e.g. Zahavi 1975; Andersson 1994; Kokko et al. 2003). The increase in reproductive success through direct benefits, i.e. through nongenetic contributions to the reproductive output of the partner or to offspring fitness, is well known concerning, for example, nuptial gifts (e.g. Gwynne 1984) or parental care (e.g. Petrie 1983). Indicator models of sexual selection (Zahavi 1975; Maynard Smith 1991; Andersson 1994; Johnstone 1995) hypothesize indirect benefits from mate preferences through genetic contributions from the partner(s) to offspring viability and/or reproductive success. Examples for indirect benefits from mate choice in several taxa are given by Møller and Alatalo (1999).

In the present study, we examined one aspect of indirect benefits for both sexes from mate preferences in *Panorpa vulgaris*. The mating system of these scorpionflies is characterized by multiple mating of both sexes, mutual mate choice and similar variances in reproductive success in both sexes (Sauer et al. 1998). Males provide the females with salivary masses during copulation. Since saliva production is costly, the number of salivary secretions produced is an indicator for the nutritional condition of a given male (Sindern et al. 1994; Sauer et al. 1998). Females of *P. vulgaris* exhibit mate choice by discriminating between males according to the number of salivary masses provided. As the number of saliva secretions determines copulation duration, which is the limiting factor in male reproductive success, differences in male investment lead to differences in male reproductive success (Sauer et al. 1990; Thornhill and Sauer 1991; Sauer et al. 1998, 1999). There is evidence that females benefit directly from mate

preference in terms of extra resources from nuptial gift consumption (Engels and Sauer 2006). Egg production of female *P. vulgaris* is, as usual in insects, condition dependent (Sauer et al. 1998) and therefore strongly connected to nutritional status. Males invest strategically into copulations with females of high fecundity exhibiting a form of cryptic male choice (Sauer 1996; Sauer et al. 1998). Thus, reproductive success of both sexes of *P. vulgaris* is, to a considerable extent, limited through mutual mate choice on the basis of nutritional condition (Sauer et al. 1998).

Could individuals also realize genetic benefits by applying these mate choice criteria? Apparently, an individual's nutritional condition is the consequence of its food acquisition success. Food acquisition in scorpionflies is composed of foraging success (Schmidt et al. 1997) on the one hand and defense/gain of food items through fighting on the other hand (Thornhill 1987; Thornhill and Sauer 1992; Bockwinkel and Sauer 1994). However, since *Panorpa* scorpionflies feed on dead arthropods (Kaltenbach 1978; Byers and Thornhill 1983; Bockwinkel and Sauer 1994), which are a temporally and spatially unpredictable distributed resource, one can expect that finding food is of equal, if not of higher, importance than winning aggressive interactions over food. In fact, the less significant role of interference competition in comparison to exploitation competition has recently been demonstrated for *P. vulgaris* and another scorpionfly, *P. communis* (Sauer et al. 2003). The authors pointed out that the interspecific level of aggression around food is low and can be essentially ruled out as being effective in reducing food acquisition success. The same holds for intraspecific interactions in both species (K.P. Sauer and A. Vermeulen, unpublished data). From this, it can be concluded that variation in condition and variation in reproductive success within a population is, to some extent, caused by variation in foraging success sensu stricto (Sindern 1996), here defined as the ability to locate dead arthropods.

Signals indicating foraging ability are well known from birds (e.g. Hill and Montgomerie 1994) and fish (e.g. Endler 1980; Houde 1997). In this context, the heritability of foraging success and its relation to male ornamentation has recently been demonstrated for the guppy *Poecilia reticulata* (Karino et al. 2005). For *P. vulgaris* scorpionflies, it can also be hypothesized that males and females may obtain indirect benefits by preferring mates of high nutritional status as this represents more skilled foraging ability and consequently may lead to higher viability and/or higher reproductive success of their offspring. However, heritability of foraging ability has not been demonstrated in *P. vulgaris* nor, as far as we know, in any other insect species. Since foraging ability is likely to be a quantitative trait, an appropriate measure of additive genetic variance is

the resemblance between parents and their offspring (Roff 1992). Therefore, in the present study, we determined foraging success of two consecutive generations of *P. vulgaris* and estimated heritability from a parent–offspring regression.

Materials and methods

Study species

The scorpionfly *P. vulgaris* is common in western Germany and lives in moist woods, shrubs and grassland communities (Sauer 1970). The diet of adults and larvae mainly consists of dead arthropods (Kaltenbach 1978; Byers and Thornhill 1983; Bockwinkel and Sauer 1993, 1994). Both sexes of *P. vulgaris* are highly promiscuous, with females mating with up to nine different males in their lifetime (Sauer et al. 1998, 1999). Males of this and other scorpionfly species exhibit enlarged salivary glands and produce salivary masses during copulation as nuptial gifts (e.g. Fleck et al. 1994; Engqvist and Sauer 2003). Besides water, the salivary secretions contain a considerable amount of protein (Fleck et al. 1996), and only males of high nutritional status are able to produce them (Bockwinkel and Sauer 1994; Sauer et al. 1997, 1998).

Breeding of the parental generation

The specimens ($n=50$ males; $n=50$ females) used in this study were reared from adult *P. vulgaris* scorpionflies of the spring generation 2004. Adults were collected in the field near Freiburg i. Br., southwest Germany. The breeding of the diapause-free developing summer generation took place at Bonn University. Briefly, the standard breeding protocol was as follows (see also Sauer 1970): Captured adults were held as pairs in $10 \times 10 \times 7$ cm plastic boxes containing moist tissue paper, ad libitum food (last instar mealworm segments, *Tenebrio molitor*) and a peat-filled Petri dish (5.5 cm diameter) for egg laying. Larvae were reared on an 18-h light/6-h dark photoperiod at 18°C on moist tissue paper with ad libitum food (see above). Immediately after moulting to the third instar larvae, individuals were transferred into soil-filled, open-bottomed plastic cylinders (40 cm diameter) placed in a field ground where development could be finished.

Immediately after hatching, adults were individually marked by painting colour spots on the forewings and transferred into outdoor population enclosures ($150 \times 70 \times 70$ cm) containing blackberry bush branches (*Rubus spec.*) and moist tissue paper providing semi-natural conditions. Males and females were held separately with each enclosure containing 50 individuals. Food was limited to

13 mealworm segments per day and enclosure, randomly attached to the blackberry bush leaves, resulting in food competition and a relatively low food supply of, on average, about one fourth segment per day and individual.

Experimental set-up

All individuals were tested for their ability to find food when they were 5 days old. The experiment was conducted as follows (see also Fig. 1): Each individual was placed on a paper sheet (DIN A4) covered by a transparent plastic box ($28 \times 17 \times 5$ cm). The paper sheet had three different markings where mealworm segments could be placed. Individuals were released to the opposite end of the sheet having the opportunity to cross the sheet for obtaining the food item. After reaching a piece of food, the individual was removed immediately and placed on the starting point again, while the mealworm segment was moved to the next marker (see Fig. 1 for the sequence of food item positions). To avoid direction preferences, the experimental set-up was rotated through 180° each time after the third mealworm segment was found, and the whole procedure started again.
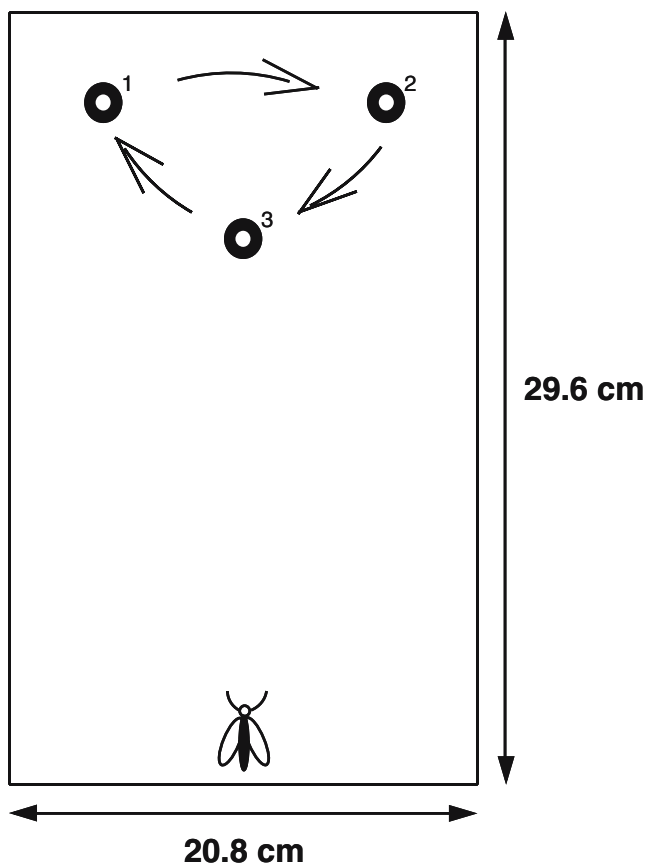

Fig. 1 Illustration of the experimental design used to determine foraging ability of individual *Panorpa* scorpionflies. For detailed description, see text

Using this approach, we defined foraging ability as the number of food items detected and approached within 3 h.

To determine the repeatability of individual foraging ability, each individual was tested again after 2 days. After reaching sexual maturity, males and females were mated assortatively according to their foraging ability. Paired males and females always descended from different pairs collected in the field.

Breeding and experimental set-up for the offspring generation

The breeding protocol for the resulting offspring was as described above, except that fourth instar larvae were transferred into soil-filled plastic cups (height, 7.5 cm; diameter, 6.8 cm) with each containing 8 to 12 larvae. Diapause-free development took place on an 18-h light/ 6-h dark photoperiod at 18°C in the laboratory. After hatching, individuals were held solitarily in small plastic tubes (height, 8.0 cm; diameter, 3.5 cm) and immediately provided with one single mealworm segment each. When individuals where 5 days old, the same experimental protocol was applied as for the parental generation. We were able to test the foraging ability of 1–24 offspring per family for a total of 38 families at 5 days of age (total $n = 702$ offspring). To determine repeatability of foraging ability for the offspring generation, we tested a subsample of $n = 86$ randomly selected individuals again after another 5 days, during which each individual was provided with another single mealworm segment.

Repeatability and heritability analyses

Repeatabilities of foraging success were calculated according to Lessells and Boag (1987) using the formula $r = [(MS_{among} - MS_{within})/n]/[((MS_{among} - MS_{within})/n) + MS_{within}]$. Variance components were estimated from a Model II analysis of variance (ANOVA). Calculation of standard errors was performed as described by Turner and Young (1969).

To estimate the heritability of foraging ability, resemblance of parents and offspring was analysed performing a parent–offspring regression. To calculate mid-parent foraging success, we used the average foraging success of both conducted trials of each parent. Since only 86 offspring were tested twice, we used values of the first trial only ($n = 702$) to calculate mean offspring family values. Narrow sense heritability (h^2 = additive genetic variance/total phenotypic variance) was calculated as the slope (b) of a regression of mean offspring foraging ability score on mid-parent foraging ability score. To correct for a bias in the estimate of heritability according to assortative mating, we used the formula $h^2 = 2b/(1+r)$ (Falconer and Mackay

1996), where r is the phenotypic correlation coefficient between parents. Additionally, we corrected the heritability estimate by weighting for families of unequal size (Sokal and Rohlf 1997).

Statistical analyses were performed using SPSS 12.0. Assumptions for parametric tests were met in all cases. All error probabilities are for two-tailed tests, and the level of significance was set to alpha ≤0.05.

Results

We measured foraging success due to the number of food items detected and approached within 3 h for a parental and the corresponding offspring generation of *P. vulgaris* scorpionflies. There was no difference in foraging ability between the sexes of both generations (male foraging ability score ±SD=1.6±2.2; females=1.5±2.2; two-way mixed-model ANOVA including family as random factor: $F_{1, 49}=0.73$; $p=0.9$). Subsequent analyses were thus performed combining the values of both sexes.

Number of food items found was significantly repeatable in the parental (r±SE= 0.21±0.096; ANOVA: $F_{99, 100}=1.53$; $p=0.018$) as well as in the offspring generation (r±SE = 0.29±0.099; ANOVA: $F_{85, 86}=1.82$; $p=0.003$). Individuals that found more food items than others in the first run of the experiment were more likely to do so in the second run.

With a parent–offspring regression, we estimated the heritability of foraging ability from the slope of the regression line. The estimate of heritability (h^2±SE=0.15± 0.046) from mid-parent and mid-offspring values was
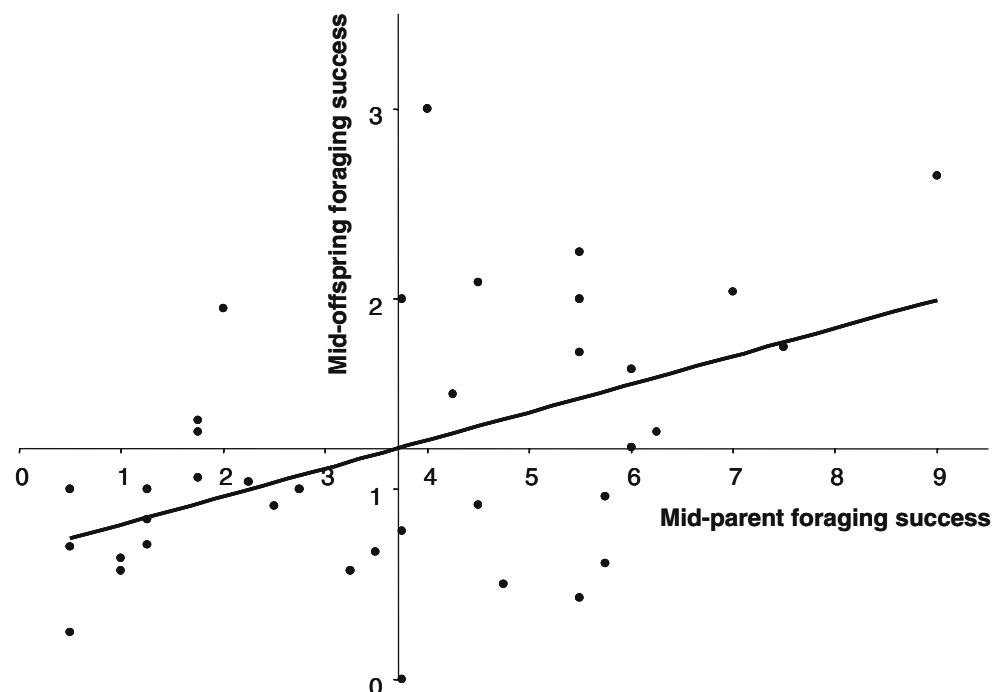
significantly different from zero ($F_{1, 36}=10.28$; $p=0.003$; see also Fig. 2); hence, offspring foraging success was affected by foraging success of the corresponding parents.

Discussion

Females of *P. vulgaris* are known to perform mate choice with respect to the saliva production ability of males (Sauer et al. 1998). Since the capability to produce salivary masses is a result of lifetime feeding history (Fleck et al. 1994), it is an indicator of individual male foraging ability (Sindern 1996). Males of *P. vulgaris*, in turn, perform mate choice by investing more nuptial gifts in females of high nutritional status that is also linked to feeding history and thereby to foraging ability of individual females (Sauer 1996; Sauer et al. 1998). Thus, it is conceivable that individuals of both sexes indirectly benefit from mate choice on the basis of nutritional condition of the partner by improving the foraging efficiency of their offspring. One necessary prerequisite for this hypothesis, however, is a heritable component of foraging ability.

The results of the present study provide not only evidence for the existence of individual differences in foraging success but also for a heritable component of this trait. The number of detected food items per time unit was significantly repeatable in parental and offspring generation, indicating the existence of individual foraging abilities in both sexes. However, repeatabilities seem to be low compared to reported repeatabilities of behavioural traits in some other species (for a review, see Boake 1989) and

Fig. 2 Narrow sense heritability (h^2) of foraging ability as estimated from a parent–offspring regression. Axes cross at overall averages. Each data point represents one family

point to a strong influence of environmental factors on individual foraging success in *P. vulgaris* scorpionflies.

There was a great difference between mean values of parent and offspring foraging success (see Fig. 2). This difference is probably due to differences in keeping conditions between the two examined generations (see Materials and methods). Being reared in a group possibly alters the motivation to forage to some extent and increases observable values of mean foraging success. However, additionally, the foraging ability of the two generations was tested during different times of the year, and *Panorpa* scorpionflies show, depending on weather conditions (even in the laboratory), very variable degrees of activity (personal observation).

The significant parent–offspring regression indicates a genetic basis of foraging ability. Hence, foraging ability as demonstrated by nuptial gift production in males or nutritional condition in females could act as an honest signal of genetic quality, and both sexes may therefore potentially profit from choosing mates with high foraging capabilities, as this should lead to an increase of foraging skills in their offspring.

This idea is compatible with what is already known about mate choice in *P. vulgaris* as there is convincing evidence for the general applicability of "good genes" models concerning mate choice behaviour in this species. Previous studies could show that females of *P. vulgaris* may indirectly benefit from choosing males capable of producing salivary secretions by increasing fighting prowess of their offspring (Thornhill and Sauer 1992; Sauer et al. 1998). Additionally, Kurtz and Sauer (1999) showed that genetic benefits in terms of higher offspring immunocompetence can potentially be obtained by both sexes. With respect to our experiment, the list of potential genetic benefits obtained by mate choice on the bases of the partner's condition may now be prolonged by "good foraging genes", i.e. another important aspect that can contribute to overall viability and reproductive success of offspring. However, it can be argued that one should not distinguish between different kinds of potential indirect benefits in this instance. This is because all "good genes" affecting condition and viability will be selected for at once by the mate choice criteria possessed. In this respect, saliva secretion ability of males and nutritional status of females would act, according to Grafen (1990) and Johnstone and Grafen (1992), as honest signals for overall genetic quality concerning viability and reproductive potential.

The heritability of foraging ability estimated in our study indicates a low proportion of additive genetic variance compared to the total phenotypic variance as expected for behavioural traits from a study by Mousseau and Roff (1987). Higher heritability estimates for foraging skills have been shown for vertebrates (e.g. Lemmon 1993; Gibbons et

al. 2005). However, as pointed out by Houle (1992), low heritability values do not necessarily mean that the total amount of additive genetic variance is low. Instead, low heritability values may also result from the fact that total phenotypic variance is especially high, which is often the case for fitness-related traits that are affected by a high number of genetic and environmental factors. Additionally, concerning the evolution of mate preferences in *P. vulgaris*, it has to be kept in mind that mate choice based on the partner's condition does not necessarily reflect mate choice based on heritable differences in foraging ability only (see above).

Further studies are needed to investigate the indirect benefits of preferring mates of high conditional status in terms of "good foraging genes" for both sexes in more detail. Based on the present study, it is not possible to decide whether inheritance of foraging ability is sex-linked. If so, indirect benefits from mate choice would apply to one sex only. Furthermore, a direct examination of the relationship between foraging success, saliva production ability of males and egg production ability of females, respectively, will help to gain more insight into the potential of indirect benefits from mate preferences in *P. vulgaris* scorpionflies.

References

Andersson M (1994) Sexual selection. Princeton Univ. Press, Princeton

Boake CRB (1989) Repeatability: its role in evolutionary studies of mating behaviour. Evol Ecol 3:173–182

Bockwinkel G, Sauer KP (1993) *Panorpa* scorpionflies foraging in spider webs—kleptoparasitism at low risk. Bull Br Arachnol Soc 9:110–112

Bockwinkel G, Sauer KP (1994) Resource dependence of male mating tactics in the scorpionfly, *Panorpa vulgaris* (Mecoptera, Panorpidae). Anim Behav 47:203–209

Byers GW, Thornhill R (1983) Biology of the Mecoptera. Ann Rev Entomol 28:203–228

Endler JA (1980) Natural selection on color patterns in *Poecilia reticulata*. Evolution 34:76–91

Engels S, Sauer KP (2006) Love for sale and its fitness benefits: nuptial gifts in the scorpionfly *Panorpa vulgaris* represent paternal investment. Behaviour 143:825–837

Engqvist L, Sauer KP (2003) Amorous scorpionflies: causes and consequences of the long pairing prelude of *Panorpa cognata*. Anim Behav 63:667–675

Falconer DS, Mackay TFC (1996) Introduction to quantitative genetics. Longman, Harlow

Fleck S, Sindern J, Sauer KP (1994) Nuptial feeding in relation to food availability in the scorpionfly Panorpa vulgaris. Verh Dtsch Zool Ges 87:36

Fleck S, Kegel G, Sauer KP (1996) The chemical composition of nuptial gifts in the scorpionfly Panorpa vulgaris (Mecoptera: Panorpidae). Verh Dtsch Zool Ges 89:241

Gibbons ME, Ferguson AM, Lee DR (2005) Both learning and heritability affect foraging behaviour of red-backed salamander, Plethodon cinerus. Anim Behav 69:721–732

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

Gwynne DT (1984) Courtship feeding increases female reproductive success in bushcrickets. Nature 307:361–363

Hill GE, Montgomerie R (1994) Plumage color signals nutritional condition in the house finch. Proc R Soc Lond B 258:47–52

Houde AE (1997) Sex, color and mate choice in guppies. Princeton Univ. Press, Princeton

Houle D (1992) Comparing evolvability and variability of quantitative traits. Genetics 130:195–204

Johnstone RA (1995) Sexual selection, honest advertisement and the handicap principle: reviewing the evidence. Biol Rev 70:1–65

Johnstone RA, Grafen A (1992) Error-prone signalling. Proc R Soc Lond B 248:229–233

Kaltenbach A (1978) Mecoptera (Schnabelhafte, Schnabelfliegen). Handb Zool 4:1–111

Karino K, Utagawa T, Shinjo S (2005) Heritability of the algal-foraging ability: an indirect benefit of female mate preference for males' carotenoid-based coloration in the guppy, Poecilia reticulata. Behav Ecol Sociobiol 59:1–5

Kokko H, Brooks R, Jennion MD, Morley J (2003) The evolution of mate choice and mating biases. Proc R Soc Lond B 270:653–664

Kurtz J, Sauer KP (1999) The immunocompetence handicap hypothesis: Testing the genetic predictions. Proc R Soc Lond B 266:2515–2522

Lemmon WC (1993) Heritability of selectively advantageous foraging behaviour in a small passerine. Evol Ecol 7:421–428

Lessels CM, Boag PT (1987) Unrepeatable repeatabilities: a common mistake. Auk 104:116–121

Maynard Smith J (1991) Theories of sexual selection. Trends Ecol Evol 6:146–151

Møller AP, Alatalo RV (1999) Good-genes effects in sexual selection. Proc R Soc Lond B 266:85–91

Mousseau TA, Roff DA (1987) Natural selection and the heritability of fitness components. Heredity 59:181–197

Petrie M (1983) Female moorhens compete for small fat males. Science 220:413–415

Roff AD (1992) The evolution of life histories: theory and analysis. Chapman and Hall, New York

Sauer KP (1970) Zur Monotopbindung einheimischer Arten der Gattung Panorpa (Mecoptera) nach Untersuchungen im Freiland und im Laboratorium. Zool Jb Syst 97:201–284

Sauer KP (1996) Sexuelle Selektion und ökologische Differenzierung. J Zoolog Syst Evol Res 34:235–249

Sauer KP, Riebel W, Bockwinkel G (1990) Influence of sequence and duration of copulation of males of Panorpa vulgaris (Mecoptera) on their paternity. Verh Dtsch Zool Ges 83:656

Sauer KP, Sindern J, Kall N (1997) Nutritional status of males and sperm transfer in the scorpionfly Panorpa vulgaris (Mecoptera: Panorpidae). Entomol Gen 31:189–204

Sauer KP, Lubjuhn T, Sindern J, Kullmann H, Kurtz J, Epplen C, Epplen JT (1998) Mating system and sexual selection in the scorpionfly Panorpa vulgaris (Mecoptera, Panorpidae). Naturwissenschaften 85:219–228

Sauer KP, Epplen C, Over I, Lubjuhn T, Schmidt A, Gerken T, Epplen JT (1999) Molecular genetic analysis of remating frequencies and sperm competition in the scorpionfly Panorpa vulgaris (Imhoff and Labram). Behaviour 136:1107–1121

Sauer KP, Vermeulen A, Aumann N (2003) Temperature-dependent competition hierarchy: a mechanism stabilizing the phenological strategy in the scorpionfly Panorpa communis L. J Zool Syst Evol Res 41:109–117

Schmidt A, Sindern J, Sauer KP (1997) The mating system of scorpionflies: no example for resource-defence-polygyny! Verh Dtsch Zool Ges 90:255

Sindern J (1996) Einfluss der Nahrungsdichte auf die Lebensge-schichte und Fitness von Individuen der Skorpionsfliege Pan-orpa vulgaris. Ph.D. thesis, Bonn University, Bonn

Sindern J, Kullmann H, Fleck S, Sauer KP (1994) Does "male choice" exist in the scorpionfly Panorpa vulgaris? Verh Dtsch Zool Ges 87:58

Sokal RR, Rohlf FJ (1997) Biometry. The principles and practice of statistics in biological research. Freeman, New York

Thornhill R (1987) The relative importance of intra- and interspecific competition in scorpionfly mating systems. Am Nat 130:711–729

Thornhill R, Sauer KP (1991) The notal organ of the scorpionfly: an adaptation to coerce mating duration. Behav Ecol 2:156–164

Thornhill R, Sauer KP (1992) Genetic sire effects on the fighting ability of sons and daughters and mating success of sons in a scorpionfly. Anim Behav 43:255–264

Turner HN, Young SSY (1969) Quantitative genetics in sheep breeding. Cornell Univ. Press, New York

Zahavi A (1975) Mate selection—a selection for handicap. J Theor Biol 53:205–214