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The evolution of sex differences in mate searching when females benefit: new theory and a comparative test

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Sexual selection is thought to have led to searching as a profitable, but risky way of males obtaining mates. While there is great variation in which sex searches, previous theory has not considered search evolution when both males and females benefit from multiple mating. We present new theory and link it with data to bridge this gap. Two different search protocols exist between species in the bush-cricket genus *Poecilimon* (Orthoptera): females search for calling males, or males search for calling females. *Poecilimon* males also transfer a costly nuptial food gift to their mates during mating. We relate variations in searching protocols to variation in nuptial gift size among 32 *Poecilimon* taxa. As predicted, taxa where females search produce significantly larger nuptial gifts than those where males search. Our model and results show that search roles can reverse when multiple mating brings about sufficiently strong material benefits to females.

Keywords: mate searching; nuptial gift; resource advertising; risk shift

1. INTRODUCTION

Although searching by males for mates is the primary mode of pair formation in most animals [1,2], in some taxa, such as anurans (frogs and toads) and orthopterans (crickets and allies), it is the female that typically searches for sedentary singing males. Variation also exists within species [2]; male crickets, for example, may switch from calling to searching when population densities are high [3]. Understanding sex-specific variations in pair formation is interesting because search effort by either sex reduces the need for the other to search [2].

What factors explain the sex roles in searching? Typically, it is argued that the sex that benefits more from multiple mating (the sexually selected sex) evolves to take more of the risk during pair formation [4,5]. Both signalling and moving towards a signal can be risky activities. For example, in taxa with sedentary singing males, predators and parasitoids can eavesdrop on signals [6]. Pheromonal signalling is thought to attract few natural enemies, resulting in a predominance of sedentary chemical signalling by females (e.g. Lepidoptera [4,5]). Empirical estimates of pair formation risk are sparse, although in several spider species where female web pheromones attract males over long distances, moving appears to be more dangerous than signalling: male mortality while searching is in excess of 70 per cent (e.g. [7,8]), which is presumably much higher than sedentary female mortality during the corresponding time. In spiders, greater male mobility has also been directly linked to higher predation [9].

With regard to singing risk exceeding searching risk, the only estimate of field mortality (in two congeneric

tettigoniid bush-crickets) was not consistent with this prediction; the pre-mating activities of the sexes imposed similar risks in *Poecilimon veluchianus* (a species in which the male sings and the female searches), whereas in *Poecilimon affinis* (a species in which most searching is by the male for the singing female) survivorship was much higher for females. As in spiders, risk in these bush-crickets was also directly related to increased movement [10].

If mate searching through moving is riskier than signalling, the question concerning which sex is expected to search remains. Here, we provide both an empirical test and new theory. Previous models by Kokko & Wong [2] showed that greater male searching evolves when there is sperm competition (i.e. multiple mating by females). However, there have been no predictions regarding outcomes when signalling trades off with mate searching or when the risk of these activities differs. Furthermore, Kokko & Wong [2] assumed that multiple mating by females did not increase fecundity. This assumption does not appear to hold for insects, especially those in which males provide a resource to their mates [11]. For example, in singing Orthoptera, males can provide a burrow as a safe haven (as in some gryllid crickets [12]), and often there is a food gift that can enhance fecundity, especially in tettigoniids and related families [11,13]. Such resources have been argued to select for females with the searching role in pair formation [4,5]. Although these roles reverse, it is not a complete reversal of roles [14–16] as in the sense of one sex becoming far less competitive about mate acquisition: our focus concerns the roles of active search (mobility) and signalling.

Sex role reversals occur in certain populations of a few tettigoniid bush-crickets when females compete for a valuable spermatophylax food gift [17]. This gift, found in most tettigoniids, is a male glandular secretion attached

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to an ejaculate-containing ampulla [18]. Together, the gift spermatophylax and the sperm ampulla comprise the spermatophore, and can show a remarkable interspecific variation in size [17,19]. The tettigoniid genus *Poecilimon* is an ideal group to test the hypothesis about male resources and mate-searching patterns because there is extensive interspecies variation in gift size (from 4 to 40% of male body mass [19]), as well as in which sex signals or searches [10].

Here, we first develop a new model for predicting sex roles in mate searching when both males and females can benefit from multiple mating. In the context of nuptial gifts, our results predict that gift size should be larger in species where females search for calling males relative to those where males search for females. We support this in a study of spermatophore gifts across 32 *Poecilimon* bush-crickets.

2. MODELLING SEARCH ROLES WITH DIRECT BENEFITS

It may sound intuitive that females should search more when multiple mating brings direct benefits, but should such a response coevolve with males switching to a different strategy? As highlighted above, there is currently no theory to answer this question. The closest model [2] allows both females and males to search for mates, and includes sperm competition, but on its own it cannot be used to answer this question because these authors assumed no benefit for females if they mate multiply. In that model, the fecundity of all females is constant regardless of the number of times she mates (beyond one; there is still potential selection for female mate-finding, though, as female fecundity was assumed zero if she failed to locate even one male during the mating window).

The model can easily be modified to include direct benefits of multiple mating. We refer to Kokko & Wong [2] for the main derivation of the model, and only briefly recap its assumptions here (see appendix for derivation). In their model, female and male mating rates m_F and m_M jointly depend on female and male search effort, which are denoted, respectively, x and y . This dependency can be additive (a function of $x + y$, such that if one sex spends much effort the other will mate even if spending no effort at all) or multiplicative (xy , in which case it is essential that both sexes spend at least some effort for mate-finding to be successful), or some other function of x and y . The 'baseline' species-specific ease with which sexes find each other in this species is M , which is low for species living at low density and possessing poor mobility, and high for the opposite end of the spectrum.

We add one new parameter to this model: a measures how much female fecundity increases with multiple mating. We set a scale for fecundity such that a once-mated female produces one unit of fecundity. For multiply mated females, we assume that fecundity equals $1 + a \ln k$, where k is the number of her mates and $a > 0$ scales the rate of fitness gain with additional matings. If $a = 0$, the model reduces back to that of Kokko & Wong [2]. It is helpful to look at some numerical examples to see how this assumption behaves. If $a = 0.05$, then a twice-mated female has fecundity $1 + 0.05 \ln(2)$, which is a 3.5 per cent increase from monandry, and a female mated

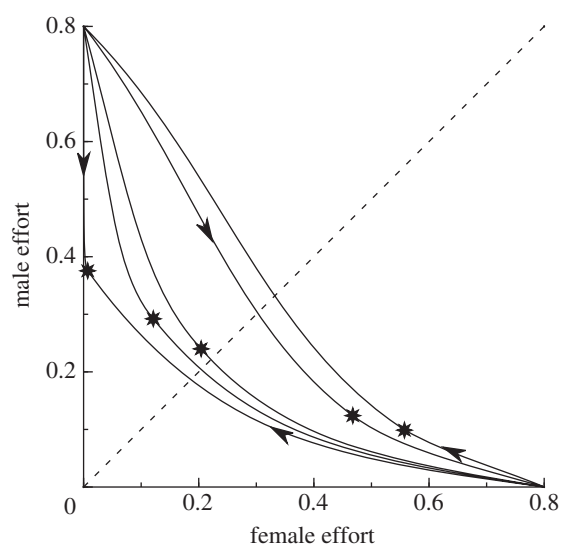


Figure 1. Evolutionary dynamics of female and male search effort for five different levels of multiple mating benefit a : from left to right $a = 0, 0.05, 0.1, 0.5$ and 1 . In each case, the baseline mate-finding efficiency is $M = 5$, and other assumptions follow fig. 5a of [2]; specifically, male 'time out' equals 0.01 time units while that of females equals 1 unit. Stable equilibria are denoted with stars, and arrows indicate the direction of evolutionary change. In the area below the diagonal line, females spend more effort mate-searching than do males.

five times shows an 8 per cent fecundity benefit. If $a = 1$, the increase for a twice-mated female is much larger at 69 per cent, and a female mated five times lays 2.6 times as many eggs as a monandrous female. Note that the logarithmic increase also includes biological realism in that the added benefit of each extra mating decelerates with more matings.

The leftmost graph of figure 1 has $a = 0$ and it reproduces exactly the $M = 5$ case in fig. 5a of [2] (effects of other parameters are explored there and we do not reproduce them here). This example assumes additivity, such that mating rates are a function of $x + y$. With $a = 0$ (i.e. no benefits of multiple mating for females), males evolve to perform all search effort (leftmost star, figure 1) regardless of whether evolution starts from a male-biased or a female-biased search scenario. For clarity, only two different arbitrary starting points are shown.

The other equilibria, from left to right, show the effects of increasing direct benefits to females (higher a). Increasing the direct benefits of multiple mating from none to a small value makes females spend more effort in searching, and males respond by searching somewhat less. Large direct benefits of multiple mating have a qualitatively similar and quantitatively stronger effect: they are sufficiently strong that the system can flip to a situation where females put more effort into searching than males. The absolute effort spent by males can now drop dramatically compared with the initial situation (where females did not benefit from multiple mating): the rightmost equilibrium in figure 1 exhibits male search effort y that equals only 26 per cent of the effort y when females did not gain anything by mating multiply.

This model does not directly comment on the nature of the search effort: the quantitative question is whether stationary calling can be understood as 'less effort' than

active mobility. Kokko & Wong [2] suggested a relatively flexible interpretation: the model is independent of the precise nature of the effort. Model assumptions will be satisfied as long as the effort increases mating rate at a cost to self (in [2] this was assumed to be a mortality cost). We have followed this assumption here, and, given that stationary calling is safer than active search, the interpretation is a switch from ‘males spend much effort, females spend no effort’ to ‘males spend only some effort, females spend much more effort than males’ (dots from left to right in figure 1) as fecundity benefits of multiple mating (parameter a) increase for females.

While figure 1 shows that the direct benefits of multiple mating can, on their own, select for high female and low male search effort, it has been derived with one potentially unrealistic assumption. The ‘time out’ of each male and female, a measure of parental investment *sensu* Clutton-Brock & Parker [20] and Parker & Simmons [21], is assumed constant across scenarios in figure 1. In other words, although there is a difference between the sexes in the ‘time out’, this difference does not covary with the direct benefits that males offer. Specifically, figure 1 assumed that male time out is only 1 per cent of that of the female. In reality, producing larger spermatophores has been argued to limit the speed with which males can return to the mating pool. This can be addressed by the model by making the time out of males covary with the parameter a . The effect of this proves to be mild, which we exemplify by making male time out identical to a except for the lowest case $a = 0$, which has a small male time out of 0.01 units. The results (figure 2) are very similar to the basic case: increasing a now makes female search effort increase even more, while the drop in male search effort is milder than in the basic case. Qualitatively speaking, the pattern is unchanged: effort becomes female-biased when direct benefits to multiple mating, a , increase sufficiently.

The above derivations are conducted with the assumption that m is proportional to $x + y$. Other formulations, such as multiplicativity (m is proportional to xy), are similarly derived and lead to the qualitatively identical conclusion that search effort becomes female-biased when a is increased sufficiently (not shown).

3. EMPIRICAL METHODS

(a) *Our study taxon: Poecilimon*

In most tettigoniids, the female searches for the calling male, but there have also been multiple origins of female acoustical answering to short male calls, followed by male searching. This variation is particularly notable in the subfamily Phaneropterinae, and especially in *Poecilimon* [22], where in some species females do not answer to male calls and instead show secondary origins of the ancestral tettigoniid pattern of female searching for the calling male [10,22–25]. The presence of both male and female searching within the same genus allows a controlled examination of hypotheses concerning sex-specific pressures that select for signalling and searching.

Our test uses field observations for 32 *Poecilimon* taxa. For all *Poecilimon* species, the spermatophylax gift is removed and eaten—often piecemeal—from the spermatophore ampulla by the female. As in other tettigoniids

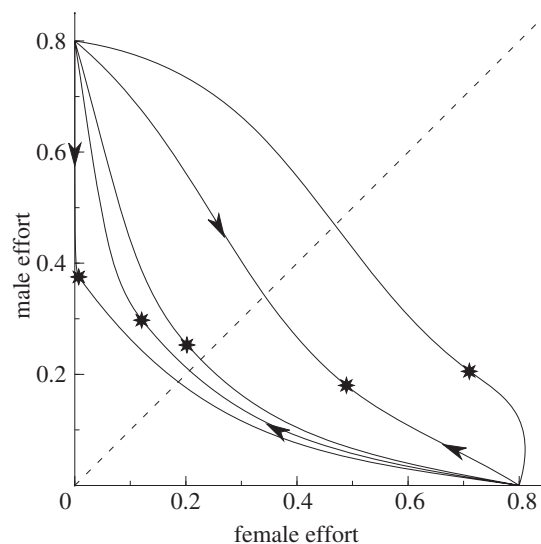


Figure 2. Evolutionary dynamics as in figure 1, but the cases $a = 0, 0.05, 0.1, 0.5$ and 1 (from left to right) are now associated with a change in the male time out such that it takes values $0.01, 0.05, 0.1, 0.5$ and 1 from left to right. Female time out is still unchanged and equals 1 across all scenarios. Other assumptions follow fig. 5a of [2].

[17], the proteinaceous ampulla is eaten once the spermatophylax is consumed. The spermatophylax meal thus protects the ejaculate (housed in the ampulla) and enhances paternity. Nutrients from the gift increase offspring fitness [26,27] (for a review see [19]). Males are known to invest heavily in both spermatophore production [23,28–31] and mate acquisition [10,22,32].

(b) *Male body mass, spermatophore size and sperm number*

Data, except those concerning which sex searches (table 1), were extracted from [19]. We included data from 32 field-observed *Poecilimon* taxa (29 species). Only species that were observed in the field had measurements of male body mass, and at least one spermatophore component were used. For most species, data were also available on spermatophylax mass, ampulla mass and sperm number. Typically, only one observation was made for each taxon by McCartney *et al.* [19], yet, in cases where more than one observation was made, priority for inclusion was first given to species data that included the most spermatophore component measurements (e.g. *P. veluchianus* [19]), then to sample size (e.g. *P. laevisimus* [19]). Data concerning searching versus signalling were determined by whether the female has sound-producing structures on her wings. The female wings in species with no response song to males (i.e. where females search for mates) are either vestigial (with no sound-producing structures) or are lost altogether [22].

All data were obtained from populations in Greece, Turkey, Italy, Slovenia or the Ukraine. Field-caught individuals were separated into cages defined by status (adults/sub-adults) and sex. Juveniles were separated until at least 7 days after their imaginal moult in order to ensure sexual maturity [27]. Adults were separated for at least 5 days prior to pairing in order to ensure full receptivity [23]. For mating, pairs were typically placed in 500 ml containers and observed either

Table 1. Male body mass, spermatophore, spermatophylax and ampulla mass and relative percentage of male body mass (rel %), sperm number and relative sperm number ($\times 10^3 \text{ mg}^{-1}$) and female acoustic response of 32 *Poecilimon* taxa.

species	male body mass		spermatophore mass		spermatophylax mass		ampulla mass		sperm number		female acoustic response	
	mg	n	mg	rel %	mg	rel %	mg	rel %	$\times 10^6$	$\times 10^3 \text{ mg}^{-1}$	n	response
<i>Poecilimon aegaeus</i>	849	10	272	31.4	236.1	27.2	34.3	4.0	—	—	7	N
<i>Poecilimon affinis</i>	1328	4	201	15.1	170.3	12.8	30.9	2.3	4.4	3.3	3	Y
<i>Poecilimon armitus</i>	410	8	68	20.5	48.0	11.7	20.0	5.3	—	—	—	N
<i>Poecilimon brunneri</i>	320	9	62	20.7	48.0	15.0	14.0	3.4	—	—	—	Y
<i>Poecilimon deplanatus</i>	449	15	41	9.2	55.0	12.3	9.0	2.0	—	—	—	Y
<i>Poecilimon ege</i>	568	4	168	28.7	140.0	24.7	28.0	4.9	11.1	19.5	3	N
<i>Poecilimon erimanthos</i>	650	25	47	7.2	42.8	6.6	4.1	0.6	0.9	1.4	19	Y
<i>Poecilimon gerlindae</i>	552	9	154	29.7	135.0	24.5	19.0	3.7	2.4	4.3	9	N
<i>Poecilimon hamatus</i>	517	5	121	22.3	110.0	21.3	11.0	2.1	0.2	0.4	4	Y
<i>Poecilimon hoelzeli</i>	2250	>10	387	17.2	381.0	12.9	61.0	2.0	13.4	6.0	3	Y
<i>Poecilimon ikariensis</i>	473	5	71	14.5	56.0	11.8	15.0	3.2	0.2	0.4	4	Y
<i>Poecilimon jonicus jonicus</i>	352	6	52	14.9	45.0	12.8	7.0	1.9	0.4	1.1	6	Y
<i>Poecilimon jonicus superbus</i>	306	2	57	18.6	—	—	—	—	0.2	0.7	4	Y
<i>Poecilimon jonicus tessellatus</i>	721	3	83	11.6	69.3	9.6	13.3	1.9	—	—	—	Y
<i>Poecilimon laevisimus</i>	781	50	48	6.1	44.0	5.6	3.7	0.5	0.7	0.9	7	Y
<i>Poecilimon macedonicus</i>	302	12	65	21.8	—	—	—	—	2.0	6.6	4	Y
<i>Poecilimon mariannae</i>	583	21	133	22.8	109.0	18.6	34.0	5.8	2.4	4.1	21	N
<i>Poecilimon marmaraensis</i>	490	8	104	21.2	73.0	14.9	31.0	6.3	—	—	—	N
<i>Poecilimon nobilis</i>	1405	6	194	13.9	158.4	11.3	35.6	2.6	6.6	4.7	13	Y
<i>Poecilimon obesus</i>	1869	5	247	13.4	209.0	11.2	38.0	2.1	4.0	2.1	10	Y
<i>Poecilimon ornatus</i>	2552	9	310	11.8	274.6	25.5	35.2	1.4	—	—	—	Y
<i>Poecilimon pergamicus</i>	174	5	53	30.4	44.0	25.3	9.0	5.2	2.8	16.1	1	N
<i>Poecilimon sanctipauli</i>	1355	1	337	24.9	316.0	23.3	21.0	1.6	2.6	1.9	1	Y
<i>Poecilimon schmidtii</i>	525	8	73	13.9	63.0	12.1	9.2	1.7	0.9	1.7	2	Y
<i>Poecilimon thessalicus</i>	464	20	112	24.0	89.0	19.2	30.0	4.3	14.0	30.2	20	N
<i>Poecilimon turcicus</i>	632	3	152	24.1	102.0	16.1	50.0	8.0	6.4	10.1	2	N
<i>Poecilimon uleranicus</i>	274	12	60	21.9	48.0	17.5	12.0	4.4	0.4	1.5	4	Y
<i>Poecilimon unispinosus</i>	404	2	82	20.3	68.0	16.8	14.0	3.5	0.9	2.2	2	Y
<i>Poecilimon veluchianus minor</i>	327	70	56	17.1	47.0	14.4	9.0	2.7	3.4	10.4	19	N
<i>Poecilimon veluchianus veluchianus</i>	710	1	182	25.6	145.0	20.4	37.0	5.3	10.4	14.6	50	N
<i>Poecilimon wermeri</i>	318	5	47	14.6	39.0	12.3	8.0	2.5	0.2	0.6	2	Y
<i>Poecilimon zimmeri</i>	818	91	146	17.8	—	—	—	—	28.4	39.9	5	N

Table 2. Differences in body mass residuals of spermatophore, spermatophylax and ampulla size, and sperm number, between groups of males that respond phonotactically to females and females that respond phonotactically to males in 32 *Poecilimon* taxa. d.f. for one-way *t*-test are based on unequal variance, not group size [40].

	males respond phonotactically			females respond phonotactically			<i>t</i> -obs	d.f.	<i>p</i> -value
	<i>n</i>	\bar{x}	s.e.	<i>n</i>	\bar{x}	s.e.			
spermatophore mass	20	-0.07	0.035	12	0.114	0.025	4.25	1,29	<0.001
spermatophylax mass	18	-0.07	0.034	11	0.111	0.029	3.98	1,26	<0.001
ampulla mass	18	-0.10	0.054	11	0.171	0.032	4.39	1,25	<0.001
sperm number	16	-0.1	0.055	9	0.177	0.055	3.45	1,20	0.001

continuously or at short intervals (e.g. 5 min) until the female carried a spermatophore. The spermatophore was subsequently removed carefully with forceps and measured at least to the nearest 1 mg. The ampulla was then dissected from the spermatophylax and both were weighed. On occasion, either the spermatophylax or the ampulla mass could not be measured; in these cases, the missing datum was calculated as the difference between the full spermatophore mass and the mass from the known component.

For *P. mariannae*, sperm counting was completed on a Coulter counter (for details of the method see [33]). For all other species, details of the method for counting sperm were standard and can be found in [19].

(c) Analysis

By comparing species within a single genus, we control, to a large extent, for similarities that may be caused by relatedness [34,35]. Ideally, phylogenetic signal should be accounted for in order to fully understand the relationship between pair-forming behaviour and spermatophore size variation across species [35–37]. While male searching is likely to have evolved independently in *Poecilimon* at least four times (*P. propinquus* group, *P. ornatus* group, *P. pergamicus* group and *P. heroicus* group [10,22,24,25,38]), insufficient data currently exist on phylogeny and spermatophore size for a comparative analysis using phylogenetically independent contrasts of *Poecilimon* taxa that differ in searching behaviour. However, while accounting for ancestry and body mass among a smaller group (23) of *Poecilimon* species for which phylogenetic relationships are known, a recent study [39] found a significant relationship between spermatophylax mass and ampulla mass. Thus, there is a strong indication that spermatophore component sizes are not confounded by ancestry, and are evolutionarily labile and responsive to selection. Furthermore, the variation in spermatophore size within *Poecilimon* approximates variation within the Tettigoniidae as a whole [19]. Given this degree of variation of species within a single genus, evolutionary history appears to have had little influence in preventing change [35].

A well-documented relationship exists between male body mass and the spermatophore components in *Poecilimon* [19,31]. This must be accounted for in analyses to obtain data on the relative allocation to the nuptial gift. Thus, to give relative component mass, all morphological data were first \log_{10} -transformed, then residuals calculated for male body mass versus spermatophore

mass, spermatophylax mass, ampulla mass and sperm number. Following Ruxton [40], we calculated the central tendency of the species using an unequal-variance, one-way *t*-test on the residuals.

4. RESULTS

As predicted, food gifts (spermatophylax size) in the group where females search for calling males were proportionally larger (mean 20% of male body mass) than those in which males search (13% of male body mass; table 2).

Consistent with the results of the model where females increase searching when benefits of multiple mating increase, we find that in *Poecilimon* taxa where females search, males produce significantly larger spermatophores (mean 24% of male body mass) and ampullae (5% of male body mass) than in taxa where males search (16% and 2% of male body mass, respectively). Males of female-search taxa also invest in ejaculates with sevenfold more sperm (mean proportional sperm number 16.6×10^5) compared with males from male-search taxa (2.4×10^5 ; table 2).

5. DISCUSSION

Compared with singing animals such as most other tettigoniids, many grylloid crickets, anurans and cicadid homopterans, there is substantial variation in which sex does most of the searching for mates within the tettigoniid genus *Poecilimon*. Our results show that in *Poecilimon* taxa where females search for calling males, males produce proportionally larger spermatophores and spermatophylax gifts than in species where males search for females. This is the first comparative evidence in support of the hypothesis, supported by our model, that searching for mates by females evolves when males offer a substantial resource that benefits the female [4,5]. Large gifts are likely to be of higher value than their size alone predicts: comparative studies of tettigoniid species in general showed that larger spermatophylaces are higher in protein and are associated with greater fecundity in females [41]. We note, however, that other comparative work with tettigoniids [42] shows that the evolution of larger spermatophylax gifts is associated with a decrease rather than an increase in female multiple mating. This may, however, be a consequence of a reduction in the potential mating frequency of males given their increased investment per mating (see [43]).

Our study adds to the field of sex differences in mate searching by adding a factor to previous models that had

not yet been included in existing theory. Modelling in this field has predominantly predicted female search when there is little sperm competition, and low densities create potential problems of sperm limitation [2]. However, this cannot explain female searching in *Poecilimon* because all sexual *Poecilimon* species appear polyandrous and show extensive sperm competition [44,45]. Instead, the results suggest direct benefits of multiple mating as a mechanism that, while being conceptually different from sperm limitation, has a similar effect in that active searching for mates improves female fitness. Our model shows that this not only increases female searching, but also can feed back to male tactics by reducing their search effort. This fits well with the observed switches to a less risky calling strategy.

Female searching for males is the dominant system of pair formation in singing grylloid and tettigoniid Orthoptera (crickets and bush-crickets, respectively). There is additional evidence supporting the idea that females switch to searching when multiple mating brings about direct benefits, because spermatophylaxes and other glandular gifts appear to have evolved in the major groups of ensiferan Orthoptera before male calling (and concomitant female searching) [12,46]. The prediction that large spermatophylax size within *Poecilimon* precedes female searching for calling males awaits additional data from other species and the development of a full phylogeny for this speciose genus. Our study is not able to determine whether a switch to female searching occurs before or after an increase in nuptial gift size. Interestingly, in fireflies (Coleoptera: Lampyridae), multiple losses of female mate searching preceded the associated losses of a nutritious spermatophore (absorbed in the female reproductive tract) [47]. However, in contrast to *Poecilimon*, non-searching female fireflies are flightless and appear to have sufficient resources for reproduction without the male spermatophore contribution, owing, for example, to a reduction in the trade-off between flight and fecundity [47].

It is likely that nuptial gift size increases both before and after the switch; once female searching evolved (as a response to this direct benefit), sexual selection could conceivably cause further increases in gift size via female choice for greater material benefits (assuming that the male phenotype honestly signals the size of his gift [17]). Female multiple mating increases sexual selection on males for a larger spermatophylax as it protects paternity (large spermatophylax meals distract females from premature consumption of the sperm ampulla). A protection role for the gift has been supported for tettigoniids (both focal and comparative studies [37,48–51], including *Poecilimon* [19,26,27,31]). Our results suggest a major role for sperm competition: *Poecilimon* species with searching females have a sevenfold increase in sperm number compared with searching males. This compares to a 2.5-fold increase in ampulla size, but only 25 per cent larger gifts.

Both paternity advantages and increased male fitness via additional gift nutrients invested into their own offspring [48,52,53] predict reproductive investment into larger gifts. Either way, producing large gifts is unlikely to be cost-free, and therefore, while not mutually exclusive with our hypothesis that direct benefits to females favour a female-search pattern, the association of small gifts with male searching could also be a consequence of

the energetic cost of searching via a trade-off. The spermatophylax gift appears to be the most energetically costly component of the spermatophore. For example, in *Poecilimon*, male mating frequency is restricted by the production of larger gifts (e.g. [43]). Gift size is also reduced when males are infected with parasites [54]. Furthermore, the higher proportions of costly proteins and nutrients in large spermatophores [55–57] indicate that the spermatophylax size might be compromised by searching effort.

On its own, this would predict that gift size is constrained by male searching effort, rather than males switching from searching to calling as the most profitable mate attraction method as females increase their search effort. It should be noted that both factors can operate simultaneously without invalidating our study, as they reinforce each other; also, the changes in the behaviour of both sexes suggest that explanations solely based on male constraints are insufficient. The main cost of search effort may also manifest itself as increased mortality instead of reduced allocation to other components of fitness (including spermatophylax traits). Studies of sex differences in mortality in a male-search and a female-search *Poecilimon* species have shown that male mortality is greater than that of the female only in a species where males search [10]. This reinforces our initial premise that searching is the riskier of the two activities, and the sex that performs this role is expected to benefit significantly from acquiring multiple mates.

How does the reversal from male to female mate-searching (for a valuable male resource) fit into a broader understanding of sex differences? Theory predicts that females may assume a male-like competitive role when resources provided by males limit female reproduction [14–16]. With the evolution of female searching for resource-providing males, the increased value of the male gift should increase the female sexual selection gradient (fecundity \times mating success regression) [58,59]. Whether sexual selection on females leads to a full reversal in the direction of sexual competition (sex role reversal) awaits behavioural studies of individual species and tests of the prediction that the slope of the female sexual selection gradient exceeds that of the male [60].

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APPENDIX A. MODEL DETAILS

The model is produced with the assumptions of Kokko & Wong [2], but changing the definition of p in their eqn (6). In Kokko & Wong's model [2], p referred to the probability that the female finds a mate during her mating window, and her fitness is directly proportional to this probability. In our current formulation, we need to specify the fitness consequences of each mate-number scenario: females mated once have relative fecundity 1, twice-mated females have fecundity $1 + a \ln 2$, thrice-mated $1 + a \ln 3$, and so on.

With a mating rate m , the probability of mating k times is Poisson-distributed with mean m , assuming that mates

are encountered randomly. This distribution specifies that the probability of exactly k matings is $m^k e^{-m}/k!$, which implies that expected female fecundity (which we still denote p to aid comparison) can be written as

$$p = \sum_{k=1}^{\infty} \frac{(1 + a \ln k) m^k e^{-m}}{k!}.$$

Inserting the expression $m = M\sqrt{a}(x+y)$, as did Kokko & Wong [2] (here β is the sex ratio self-consistently derived from the two-sex dynamics; see their appendix), leads to the expression for $\partial p/\partial x$ that is needed to modify eqn. (6) in [2]:

$$\frac{\partial p}{\partial x} = \sum_{k=1}^{\infty} \frac{(1 + a \ln k) M \sqrt{\beta} m^{k-1} (m - k) e^{-m}}{k!},$$

where $m = \sqrt{\beta}(x+y)$.

This infinite sum unfortunately does not converge to a simple analytical solution; however, its values are easily derived numerically.

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