R E V I E W

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Polyandry and fecundity in the Lepidoptera: can methodological and conceptual approaches bias outcomes?

Abstract Polyandry is a reproductive strategy whose occurrence has been explained in terms of both direct and indirect benefits to females. Among the direct benefits, a positive correlation between female remating and fecundity, mediated by receipt of nuptial gifts, is considered a major factor maintaining polyandry. However, a careful inspection of available studies reveals that such a correlation is not universal. In this comparative study of Lepidopterans we analysed two-way contingence tables based on 60 studies, and performed a meta-analysis of 39 studies to document associations between (1) the mating pattern (monandrous or polyandrous); (2) the methodological approach used (experimental or descriptive); and (3) the effect of female remating on fecundity. All three variables were significantly associated. Studies where remating increased fecundity were more often established in polyandrous species and when the experimental method was used. However, the experimental method also tended to be utilised more often for polyandrous species. Meta-analysis confirmed these 'vote-count'-based associations. We were also able to differentiate the relative effects of mating pattern and methodology on the remating-fecundity relationship. In polyandrous species, remating increased fecundity irrespective of the test method. In monandrous species, however, conclusions were method-dependent: fecundity did not increase with remating in descriptive studies. We discuss some biological and non-biological factors that may account for these heterogeneous results. We suggest that greater attention must be paid to variation among females in their propensity to mate multiply. The mating pattern of a species will influence the conclusions drawn from experimental and descriptive studies of the relationship between polyandry and fecundity because it covaries with the proportion of naturally monandrous females in that species.

Keywords Polyandry · Fecundity · Experimental method · Descriptive method · Meta-analysis

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Introduction

In insects, polyandry, i.e. females multiply mating with more than one male, is a reproductive strategy that has generated considerable research because its widespread occurrence puzzles evolutionary biologists. The best male strategy to maximize reproductive output is usually to obtain as many mates as possible (polygyny), but the benefits of remating to females are less clear. In addition, levels of polyandry vary widely, not only among, but also within, species (Drummond 1984; Eberhard 1985; Ridley 1988), suggesting that any benefits of polyandry vary depending on the exact context. The fitness and evolutionary implications of polyandry have generated a huge amount of experimental and theoretical work to explain the ultimate cause(s) of female remating behaviour (Parker 1970; Walker 1980; Hunter et al. 1993; Boggs 1995; Keller and Reeve 1995; Eberhard 1996; Choe and Crespi 1997; Simmons and Siva-Jothy 1998; Vahed 1998; Yasui 1998; Jennions and Petrie 2000; Kondoh 2001; Simmons 2001; Zeh and Zeh 2001). Two main, but not mutually exclusive, lines of research have typically characterised these scenarios. The first investigates direct benefits derived from nutrient acquisition via ejaculate,

often referred to as male nuptial gifts, that improve female fecundity, offspring quality or both. The second, from which there is far less available evidence, investigates the role of indirect benefits derived from increased offspring genetic variability, obtaining 'good genes' or the avoidance of genetic incompatibility. Sperm competition and cryptic female choice are recognised as major driving forces related to indirect benefits.

A positive association between female mating frequency and increased fecundity is probably the most quantitatively important, short-term process sustaining the direct benefit hypothesis in insects. This biological correlation is supported by several primary studies (see text below), narrative reviews (Ridley 1988; Vahed 1998) and a recent meta-analysis by Arnqvist and Nilsson (2000) showing that females gain directly from multiple mating in terms of increased reproductive output. However, a careful inspection of available studies, at least for Lepidoptera, still reveals that a positive correlation between female multiple mating and fecundity is not always apparent. In particular, such a relationship appears to be less common in normally monandrous or mildly polyandrous species. As such, the occurrence of polyandrous females in these species is poorly explained in terms of a fecundity advantage.

In this study, we tested whether there is an association between the species' mating pattern (polyandry or monandry) and increased fecundity in the Lepidoptera, analysing at the same time the impact of some potentially biasing factors, particularly whether the methodological approach used critically influences the research outcome.

Methods

We compiled data from 60 studies of Lepidoptera that related female multiple mating to reproductive output (see Table 1). Information sources we searched included scientific literature databases, the Internet and previous reviews on this topic (Ridley 1988, Vahed 1998, Arnqvist and Nilsson 2000). Studies were included when three basic pieces of information were available or directly estimable: the species mating pattern; the methodological approach utilised; and the strength of the effect of female multiple mating on reproductive output.

The species' mating pattern

Species were classified according to the frequency of polyandrous females (percentage polyandry) documented in each study. When the polyandry level was not reported or was unclear for a given study, an estimate of female remating frequency for the species in question was taken from other sources (see Table 1). Species were placed in one of two mating-pattern classes. The first included both usually monandrous (<25% polyandry) and mildly polyandrous (25–40%) species. These species were simply labelled 'monandrous'. The second mating-pattern class consisted of species in which the occurrence of polyandry was higher (>40%) and these were labelled 'polyandrous'. We recognise that our criterion is somewhat arbitrary because there is no clear discontinuity in the distribution of mating frequencies across species (Ridley 1988) and, moreover, there is evidence for heritable variation within species in female propensity to mate polyandrously (e.g. Torres-Vila et al. 2002). Our justification, however, was as follows: mildly polyan-

drous species exhibiting 25–40% polyandry levels were categorised as monandrous in order to adopt a conservative approach because, under laboratory conditions (which applied to most studies in Table 1), female remating is often unnaturally enhanced as a consequence of male-female cohabitation, higher population density and/or a male-biased sex ratio. We also looked for a threshold value that did not create an unduly small pool of species categorised as monandrous. Finally, the 40% polyandry level broadly agrees with frequencies subjectively used by most other authors to categorise their target species as monandrous or polyandrous.

The methodological approach

Every study was classified according to whether its methodological approach was experimental or descriptive (Lehner 1996). Experimental studies involve the creation of two groups of randomly chosen females. In the first 'experimental' group females are allowed to mate multiply, while in the second 'control' group females are only allowed to mate once and are then isolated with no further access to males for the remainder of their lifetime. The experimental method implies that the researcher has designed the experiment a priori and randomly established female groups whose fecundity can then be compared.

In contrast, in studies that use a descriptive method, females are provided with mating opportunities throughout their lifetime. The number of matings for each female is calculated either by visual observations or by waiting until a female dies and then counting the number of spermatophores she contains. The descriptive approach implies that the test groups to be compared are established a posteriori, and that the researcher does not determine their membership. For both methods, the mean fecundity of females from the two groups (once-mated or multiply-mated) is compared to assess the effect of remating on fecundity.

Most studies (Table 1) could be unambiguously assigned as either experimental or descriptive studies as described above. In some cases, however, although the test method did not exactly fit the experimental approach (noted as 'sub-experimental' in Table 1) they were treated as experimental in our analyses because some females were only allowed to mate once. In 3 of the 60 studies, adults were manually forced to mate through the use of the hand-pairing technique to promote differences in the number of matings per female. This may influence the estimate of the effect of polyandry on fecundity because some females in the double-mated group were unnaturally forced to remate (see Discussion). Even so, these studies fulfil our definition of ones pursuing an experimental approach because females were assigned to mating categories a priori. In other studies, the effect of multiple mating on fecundity was indirectly estimated by dissection of wild-caught females to measure the change in the number of mature eggs stored in the ovaries across age-classes in relation to the number of spermatophores present in the female's bursa copulatrix. These studies were classified as descriptive because we assumed that males were available in the wild and females were allowed to freely choose their number of mates.

The effect of mating pattern on reproductive output

The occurrence of a significant positive correlation ($P<0.05$) between multiple mating and reproductive output was directly retrieved from results given by authors in each paper. In a few cases, however, especially in earlier studies, information about statistical significance was lacking, so correlation was inferred as biologically relevant based on additional information supplied by the authors or obtained from other related studies. Female reproductive output was mainly assessed in terms of fecundity (total egg number laid) or viable offspring produced, although in some cases only partial fecundity was available (realised fecundity over a fixed time period). Percentage fertility was used as an estimator of female reproductive output in six cases (see Table 1).

Table 1 Published research exploring the effect of female multiple mating on increased fecundity in Lepidoptera species. Mating pattern (monandry vs. polyandry), methodological approach (experimental vs. descriptive) and effect of female remating on fecundity is given for each study

Reference number	Species	Family	Mating pattern [a]	Percentage polyandry [b]	Method [c]	Effect of remating on fecundity	References
1	*Acrolepia assectella*	Yponomeutidae	M	38	D	No	Thibout 1975, 1978
2	*Adoxophyes orana*	Tortricidae	P	64	E[d]	Yes	Van der Kraan and Van der Straten 1988
3	*Antheraea mylitta*	Saturniidae	P?		E[e]	Yes	Ravi Kumar et al. 1995
4	*Atrophaneura alcinous*	Papilionidae	M	16	E[e]	No	Matsumoto and Suzuki 1992; Kawagoe et al. 2001
5	*Atteva punctella*	Yponomeutidae	M	9–36	D	No[f]	Taylor 1967
6	*Bicyclus anynana*	Satyridae	M	27–29	D	No?	Brakefield et al. 2001
7	*Busseola fusca*	Noctuidae	P	(2.0)	D	No[f]	Unnithan and Paye 1990
8	*Choristoneura fumiferana*	Tortricidae	P	26–63	D	Yes	Delisle and Hardy 1997; J. Delisle personal communication
9	*Colias erate* (alba morph)	Pieridae	P	40	D	Yes[g,h]	Nakanishi et al. 2000
10	*Colias erate* (yellow morph)		P	41	D	No[h]	Nakanishi et al. 2000
11	*Danaus plexippus*	Danaidae	P	63	E	No	Svärd and Wiklund 1988
12			P	95	E	Yes	Oberhauser 1989
13	*Diparopsis castanea*	Noctuidae	P	47	D	No	Marks 1976
14	*Earias insulana*	Noctuidae	P	(2.0)	E	Yes	Tamhankar 1995
15			P	(2.0)	D	Yes	Tamhankar 1995
16			P	(1.7–2.6)	D	No	Kehat and Gordon 1977
17	*Earias vittella*	Noctuidae	P	80	D	Yes	Tamhankar et al. 1993
18	*Epiphyas postvittana*	Tortricidae	P	60	E[d]	Yes	Danthanarayana and Gu 1991
19	*Euphydryas editha*	Nymphalidae	M	31	D	No	Labine 1966
20	*Helicoverpa armigera*	Noctuidae	P	68	E	Yes	Hou and Sheng 1999
21			P		D	No	Mourikis and Vassilaina-Alexopoulou 1970
22	*Heliothis virescens*	Noctuidae	P	46–71	E	No	Hendricks et al. 1970; Raulston et al. 1975; Pair et al. 1977
23	*Laspeyresia pomonella*	Tortricidae	M	27–44	D	No	Esteban-Durán 1975
24	*Lobesia botrana*	Tortricidae	M	20–35	D	No	Torres-Vila, unpublished data
25		Tortricidae	M	20–35	E	Yes	Torres-Vila, unpublished data
26	*Lymantria dispar*	Lymantriidae	M	'low'	E[i]	Yes[i]	Proshold and Bernon 1994
27	*Orgya pseudotsugata*	Lymantriidae	M	27	D	No[f]	Swaby et al. 1987
28	*Ostrinia nubilalis*	Pyralidae	M	11–38	E[d]	Yes	Fadamiro and Baker 1999
29			M	7–26	D	No	Gohari and Hawlitzky 1986
30	*Papilio glaucus*	Papilionidae	P	65	D	Yes[f,g]	Lederhouse and Scriber 1987
31	*Papilio polyxenes*	Papilionidae	M	31	D	Yes[f,g]	Lederhouse 1981
32	*Papilio xuthus*	Papilionidae	P	(>>1.5)	E[e]	Yes	Watanabe and Nozato 1986; Watanabe 1988
33	*Pectinophora gossypiella*	Gelechiidae	P[j]	'high'	E	Yes?	Bartlett and Lewis 1985
34			P[j]	(1.4–2.4)	E	No	Henneberry and Leal 1979
35	*Pieris napi*	Pieridae	P	93	E	Yes	Wiklund et al. 1993
36			P		E	Yes	Karlsson 1998
37			P		E	Yes	Wiklund et al. 1998
38			P	47–60	E	Yes[k]	Bergström and Wiklund 2002
39			P	47–60	D	Yes	Bergström and Wiklund 2002
40	*Pieris rapae*	Pieridae	P	(1.5–2.0)	D	Yes[h]	Watanabe and Ando 1993
41	*Platyptilia carduidactyla*	Pterophoridae	M?		D	No	Bragg 1970
42	*Plodia interpunctella*	Pyralidae	P	58	E	No	Cook 1999
43			P	58	D	No	Cook 1999
44			P	(2.0–2.5)	D	No	Brower 1975
45			P	(2.0–2.5)	E	No	Brower 1975
46	*Pseudaletia unipuncta*	Noctuidae	P	55	E	Yes	Callahan and Chapin 1960; Svärd and McNeil 1994
47	*Pseudoplusia includens*	Noctuidae	P[l]	10–44	D	Yes	Jensen et al. 1974
48	*Sitotroga cerealella*	Gelechiidae	P	65–72	D	Yes	Stockel 1973
49	*Spodoptera exigua*	Noctuidae	P	55	D	Yes[m]	Rogers and Marti 1996
50	*Spodoptera frugiperda*	Noctuidae	P	60	D	Yes[m]	Rogers and Marti 1994
51			P	89	E	Yes	Snow et al. 1970

Table 1 (continued)

Refer-ence number	Species	Family	Mating pattern [a]	Percentage polyandry[b]	Method[c]	Effect of remating on fecundity	References
52			P	53	D	No	Martin et al. 1989
53	*Spodoptera littoralis*	Noctuidae	P	(1.8–2.2)	E	No	Kehat and Gordon 1975
54	*Spodoptera litura*	Noctuidae	P	50–52	E[d]	Yes	Chu and Yang 1991; Takeuchi and Miyashita 1975
55	*Synanthedon exitiosa*	Sesiidae	P	50	D	No[f]	Smith 1970
56	*Trichoplusia ni*	Noctuidae	P	81	E	Yes	Ward and Landolt 1995
57			P		E	Yes	Landolt 1997
58			P	47	D	Yes	Shorey 1963
59	*Utethesia ornatrix*	Arctiidae	P	63–87	D	Yes	Pease 1968; Lamunyon 1997
60	*Zeiraphera diniana*	Tortricidae	M	21	D	No	Benz 1969

[a] *M* Monandrous; *P* polyandrous, using a 40% polyandry threshold (see text). When a range of polyandry values, including 40% threshold, occurred in a given study, average polyandry was used for monandry/polyandry assignment

[b] Percentage polyandry on mated females. Mean number of spermatophores per female is given in *brackets* when percentage polyandry was unknown

[c] *E* experimental method; *D* descriptive method

[d] Sub-experimental method. There were not two randomly chosen groups of females to be compared, but some females were deprived of males to increase the frequency of once-mated females

[e] Hand-pairing technique was used

[f] Female reproductive output was assessed in terms of fertility

[g] Differences in fecundity were only significant in the older age classes

[h] Reproductive output was estimated indirectly by dissection of wild-caught females as the change in the number of mature eggs stored in the ovaries

[i] First-male sperm manipulation. Reproductive output was estimated as egg mass (mg)

[j] Species was polyandrous in these studies [see also report of 74–88% polyandry by Henneberry and Clayton (1983)], but monandrous in others [18% in Graham et al. (1965), 28–29% in Lukefahr and Griffin (1957) and 29% in Ouye et al. (1964)]

[k] $P=0.051$

[l] A polyandrous mating pattern in this study was unclear, but this species was clearly polyandrous in other studies [e.g. 87% polyandry in Mason and Pashley (1991)]

[m] Female delayed mating in these studies may have had a confounding effect

Data analysis

Initially we used Fisher's exact probability tests (two-tailed) applied to the entire sample ($n=60$ cases; Table 1) to test for pairwise associations between the three dichotomous variables, species' mating pattern (monandry or polyandry), methodological approach (experimental or descriptive) and occurrence of a positive correlation between polyandry and fecundity (yes or no) (Scherrer 1984). This 'vote counting' approach in which studies are categorised as yielding significant or non-significant findings is problematic, however, because it ignores both information on the strength of the reported effect and the accuracy with which it is estimated (i.e. it does not take into consideration sample size) (Rosenberg et al. 2000).

To substantiate these 'vote-counting' associations, and to calculate the independent effects of species' mating pattern and test methodology respectively on the correlation between female multiple mating and fecundity, we also conducted meta-analyses. We used data from 39 studies where we could calculate an effect size for the remating-fecundity relationship (Table 2). In these studies, information on sample sizes, mean reproductive output for once-mated and multiply-mated females, and a statistical measure of its dispersion was either retrieved from the text and tables or indirectly obtained by measuring figures. For each study we calculated Hedges' unbiased effect size estimator (d) where:

$$d = \left(1 - \frac{3}{4(n_p + n_m) - 9}\right)g$$

and g is the standardised mean difference between the two groups $g=[(M_p - M_m)/\text{SD}]$, n_p and n_m are the sample sizes, and M_p and M_m the mean reproductive outputs of polyandrous and monandrous females respectively, and SD is the pooled standard deviation for the two groups (see Rosenberg et al. 2000). We treated effect sizes

from different studies (or tests using a different method from the same study) as statistically independent data points. In most cases, there was only one study per method per species, so meta-analyses based on the mean effect size per species per method yielded identical conclusions.

To test the effect of methodology and to control more fully for variation in effect size among species, we examined the six species for which effect sizes for both descriptive and experimental studies were available and could therefore be paired. We calculated the difference in average effect size per method for each species (= Cohen's q). We then tested whether the mean difference was significantly greater or less than zero.

We calculated mean effect sizes weighted for sample size (sampling variance) using the software package MetaWin 2.0 (Rosenberg et al. 2000). We always ran random effects models that allow for a true random component, in addition to sampling error, as a source of variation in effect size among studies (Hedges and Olkin 1985). We report the mean effect size and 95% confidence intervals calculated using a bias-corrected bootstrap approach (5,000 replicates), as well as the within-group heterogeneity (Q_w) for each group of studies assuming Q_w follows a Chi-square distribution, with df=Number of studies−1. We tested whether mean effect size differed between groups by testing for significance between-group heterogeneity (Q_b) using randomisation tests based on 5,000 replicates. All tests are two-tailed. We calculated Rosenthal's fail-safe number, which is an estimate of the number of additional, unpublished studies with a mean effect of zero required to turn a significant mean effect size into one that does not differ significantly from zero given $\alpha=0.05$. By convention, a value of $5n_e+10$ is considered robust (where n_e=number of studies used to calculate the mean effect size). Finally, to indirectly test for publication bias we calculated the Begg-Mazumdar correlation between standardised effect size and sample size. This should be

Table 2 The subset of 39 studies from Table 1 for which we were able to calculate effect size (Hedge's d) for the remating-fecundity relationship. n_m and n_p, M_m and M_p, and SD_m and SD_p are sample size, mean and standard deviation of reproductive output for monandrous and polyandrous groups, respectively

Reference number.	Species	n_m	n_p	M_m	M_p	SD_m	SD_p	Hedge's d
1	*Acrolepia assectella*	79	43	178	181	47	44	0.06
3	*Antheraea mylitta*	90	90	217	282	21	21	3.08
4	*Atrophaneura alcinous*	62	46	52	55	47	56	0.06
8	*Choristoneura fumiferana*	198	66	275	309	82	94	0.40
9	*Colias erate* (alba morph)	10	65	387	608	150	63	2.77
10	*Colias erate* (yellow morph)	7	19	539	587	70	71	0.66
11	*Danaus plexippus* [a]	12	19	640	678	326	572	0.08
12		12	13	397	569	197	188	0.86
14	*Earias insulana*	20	21	98	374	87	187	1.84
15		12	21	113	374	70	187	1.63
17	*Earias vittella*	44	25	215	325	85	113	1.13
18	*Epiphyas postvittana*	40	40	493	623	316	246	0.45
19	*Euphydryas editha*	9	9	1,011	912	113	207	-0.57
20	*Helicoverpa armigera*	11	23	876	1,070	740	695	0.27
24	*Lobesia botrana*	48	111	163	166	53	42	0.07
25		120	111	131	166	56	42	0.70
26	*Lymantria dispar*	65	85	430	630	260	170	0.93
28	*Ostrinia nubilalis*	48	15	540	630	292	181	0.33
29		69	11					0.31[b]
32	*Papilio xuthus*	22	15	38	50	18	23	0.58
35	*Pieris napi*	22	25	284	490	143	131	1.48
36		7	7	322	503	102	48	2.13
37		10	7	342	461	152	111	0.82
38		99	91	342	393	133	151	0.36
39		79	91	304	393	141	151	0.61
42	*Plodia interpunctella*	32	26	223	138	96	158	−0.66
43		55	26	145	138	94	158	−0.06
44		4	11	326	321	76	52	−0.08
45		24	11	285	321	108	52	0.37
46	*Pseudaletia unipuncta*	23	24	1,618	2,043	472	514	0.85
48	*Sitotroga cerealella*	26	61	115	184	55	69	1.05
49	*Spodoptera exigua*	145	176	500	835	388	387	0.86
51	*Spodoptera frugiperda*	126	168	825	1,000	520	599	0.31
53	*Spodoptera littoralis*	10	10	1,705	1,756	392	376	0.13
56	*Trichoplusia ni*	36	69	1,439	1,623	281	287	0.64
57		56	12	1,088	1,533	520	321	0.89
58		10	8	679	1,030	278	206	1.34
59	*Utethesia ornatrix*	45	76	240	62	302	75	−0.92
60	*Zeiraphera diniana*	61	13	147	144	42	50	−0.07

[a] See also Arnqvist and Nilsson (2000)
[b] In this correlational study g was estimated from the weighted Pearson correlation coefficient $r=g/(g^2+4)^{0.5}$. g was then converted to Hedges' unbiased effect size estimator d (see text)

viewed with caution, however, as this test has low statistical power with sample sizes less than 25 (Møller and Jennions 2001).

Results

The data used in our analyses were retrieved from 60 studies of 41 Lepidopteran species from 15 families (see Table 1). First, a significant positive correlation between remating and fecundity was significantly more often reported in studies of polyandrous species (30 of 45 studies, 66.7%) than of monandrous species (4 of 15 studies, 26.7%) (Fisher's exact test, P=0.014). Second, a significant positive correlation between remating and fecundity was also significantly more often reported in studies using an experimental (20 of 27 studies, 74.1%) rather than a descriptive approach (14 of 33 studies, 42.4%) (Fisher's exact test, P=0.019). This initially suggests that a positive effect of remating on fecundity is more likely to occur when a study uses an experimental approach. There was no significant association between species mating pattern and the methodological approach used when all studies were considered: the descriptive approach was used in 73.4% of studies (n=11 of 15) of monandrous species and 48.9% (n=22 of 45) of studies of polyandrous species (Fisher's exact test, P=0.14). The association was, however, significant if studies that were not strictly experimental were excluded (i.e. those scored as sub-experimental, hand-pairing-based or involving sperm manipulation, see Table 1), because 55.0% of studies of polyandrous species were descriptive (22 of 40) compared to 91.7% of studies of monandrous species (11 of 12 studies) (Fisher's exact, P=0.037). Given the more extensive use of the descriptive method when working with monandrous species, it is difficult to determine the independent effects of methodology and species mating pattern on the remating-fecundity relationship. We therefore used meta-analyses to analyse the effect of methodology for each mating type separately.

Table 3 Effect size estimates for the relationship between female remating and reproductive output in Lepidoptera species based on random effects models (see text). Data were grouped on the basis of mating pattern (monandry vs. polyandry) and test method (exper- imental vs. descriptive). n_e Number of effect sizes/studies; n total sample size. *Hedge's d* mean effect size with 95% bias-corrected bootstrapped confidence intervals

Mating pattern	Test method	Sample size		Effect size	Effect size heterogeneity			Rosenthal's
		n_e	n	Hedges's d (95% CI)	Q_w	df	P	Failsafe number
Both	Both	39	3,608	0.63 (0.40–0.90)	47.90	38	0.13	3,078[b]
Polyandrous	Both	30	2,603	0.77 (0.47–1.09)	33.48	29	0.26	2,308[b]
Polyandrous	Experimental	18	1,323	0.78 (0.44–1.22)	15.81	17	0.54	811[b]
Polyandrous	Descriptive	12	1,280	0.74 (0.24–1.23)	15.68	11	0.15	370[b]
Monandrous	Both	9	1,005	0.27 (−0.02–0.50) NS	7.40	8	0.49	–
Monandrous	Experimental	4	552	0.51 (0.19–0.87)	3.02	3	0.39	49[b]
Monandrous	Descriptive[a]	5	453	−0.01 (−0.29–0.18) NS	2.57	4	0.63	–

[a] The pooled variance was less than zero, so data were analysed using a fixed effects model
[b] Failsafe number was greater than $5n_e+10$

We calculated the effect size for the remating-fecun- dity relationship for 39 studies (Table 2). Mean effect sizes for all studies and studies divided on the basis of species' mating pattern, methodology and the four combinations of these two factors are presented in Table 3. Across all studies, remating significantly increased female fecundity by a factor of about 0.63 standard deviations. There was some heterogeneity in effect sizes among studies, but it was not greater than expected due to sampling error (Q_w=47.9, df=38, P=0.13). The mean effect size was similar for polyandrous species irrespective of methodology (d=0.74–0.78), but there was no significant increase in fecundity with remating for descriptive studies of monandrous species (d=−0.29 to 0.18, 95% CI, n_e=5) or for all studies of monandrous species (d=−0.02 to 0.50, 95% CI, n_e=9). Aside from the latter two groups, the five other estimates of effect size all had large fail-safe numbers, indicating they were robust estimates (Table 3).

In agreement with the 'vote-counting' results, the mean effect size for studies of polyandrous species was greater than that for studies of monandrous species when methodology was ignored, but the difference was not significant (Q_b=3.77, P=0.09). Because methodology and species' mating pattern are confounded, we then con- trolled for methodology. There was no significant differ- ence in effect sizes between species with polyandrous or monandrous mating patterns when considering only experimental studies (Q_b=0.40, P=0.54). The effect size for polyandrous species was larger than that for monan- drous species when considering only descriptive studies, but the difference was not significant (Q_b=4.15, P=0.10).

In contrast to the 'vote-counting' approach, when species' mating pattern was ignored there was no difference in effect size between descriptive and exper- imental studies (Q_b=0.78, P=0.45). Again, because meth- odology and species' mating pattern are confounded, we then controlled for the latter. There was no difference in effect sizes between methodologies for polyandrous species (Q_b=0.01, P=0.93). There was, however, a greater effect size for experimental compared to descriptive studies of monandrous species, although the difference

was not significant (Q_b=5.41, P=0.08). Finally, there was no difference in effect sizes for the six species where both methods were used (Cohen q=−0.05 to 0.25, 95% CI, n_e=6).

There was no significant correlation between stan- dardised effect size and sample size in any of the seven groupings of the data presented in Table 3 (P=0.14–0.71). This suggests that there is no publication bias, but this conclusion is weak because of low statistical power.

Discussion

In general, our results based on the 'vote-counting' and meta-analyses approaches suggest that there is a positive effect of female remating on increased fecundity, irre- spective of species' mating pattern or methodology. This relationship was, however, not significant for monandrous species tested using the descriptive method. It seemed to be slightly stronger in polyandrous than in monandrous species, but only when considering descriptive studies. There was no effect of methodology on the remating- fecundity relationship for polyandrous species. The effect size was greater for experimental than descriptive studies of monandrous species, but not significantly so (P=0.08). Finally, researchers significantly more often used a descriptive approach when studying monandrous species if strictly non-experimental studies were excluded from the analysis (P=0.037).

The mating pattern and the effect of remating
on reproductive output

It is widely recognised that, in insects, female remating may increase reproductive output via male-derived nup- tial gifts transferred at mating or by replenishing sperm supplies (see reviews by Ridley 1988; Vahed 1998; Arnqvist and Nilsson 2000). Our results are, in general, consistent with this notion but also provide some support for an association between the species-specific mating pattern and the relative effect of remating on increased

fecundity, as previously suggested by Ridley (1988). Overall, a significant increase in fecundity following female remating was more often reported in polyandrous than in monandrous species. Using meta-analysis we found no difference in the strength of the relationship between species types for experimental studies ($P=0.54$), and a greater, albeit non-significant, difference ($P=0.10$) for descriptive studies. Remating had no detectable effect on fecundity in descriptive studies of monandrous species. This finding suggests that factors other than species-specific attributes such as the amount of nuptial gifts, duration of the refractory period extent and optimal remating rate (Arnqvist and Nilsson 2000) should be considered when calculating the benefits of polyandry because control (monandrous) and experimental (polyandrous) groups in descriptive studies are, by definition, not selected randomly.

A stronger association between remating and increased fecundity in polyandrous species is not surprising in evolutionary terms. Leaving sexual conflict aside, one might expect polyandry to evolve because female remating is positively connected with fecundity in a given ecological context, and fecundity is a key fitness variable in insects. If female remating enhances individual fitness via fecundity, genes for a propensity to remate will be selected for and spread quickly, leading to a species (or population) becoming more polyandrous. The association between mating type and the effects of remating reported in the analysed sample occurred despite several factors that potentially bias estimates of polyandry. For example, male cohabitation, high population density and male-biased sex ratios may unnaturally increase female remating propensity in the laboratory, biasing the division of species into the categories polyandrous and monandrous (Eberhard 1985; several studies in Table 1). True polyandry may also be strongly overestimated if double or multiple mating is merely a result of unrecorded first mating failure (Ridley 1988; Torres-Vila et al. 2002 and references therein).

The association between mating pattern and test method

Our results suggest that descriptive methods are more often used when studying monandrous species. There are at least three likely reasons for this association. First, a strictly experimental approach is difficult to employ in monandrous species because many females assigned to mate multiply will fail to do so. Second, fewer studies (ca. 25%, see Table 1) of the benefits of polyandry are carried out on monandrous species. This probably occurs either because the low frequency of polyandrous females hinders statistical analysis or because such investigations have been considered irrelevant in monandrous species. When publications do report the effect of remating on fecundity in a monandrous species it is often an incidental side issue and therefore more often involves a descriptive approach. Third, papers that report the effect of remating on fecundity sometimes come from studies of sperm competition. Data on the fecundity of double-mated females from reciprocal crosses is usually collected incidentally. If, however, data on the fecundity of once-mated females is also available the comparison is, by definition, between two experimentally created groups. Studies of sperm competition typically use polyandrous species (Simmons 2001), thereby inflating the use of the experimental method for species with higher female mating rates.

Can methodological approach affect research outcomes?

The most interesting non-biological association we observed was that the test method may affect the polyandry-fecundity relationship, at least in monandrous species. A benefit of remating in terms of increased fecundity was supported in polyandrous species irrespective of the test method used. In monandrous species, however, no benefit was detectable when a descriptive method was used. It follows that substantially different conclusions could emerge for the same target species depending on the methodology chosen. This finding is not trivial, as it may lead to the available literature being misinterpreted.

An experimental approach is usually regarded as the preferred way to test whether remating enhances fecundity because it eliminates confounding factors that might covary with female mating rate and confuse the interpretation of a purely descriptive study. Ridley (1988) coined the terms 'experimental comparison' and 'non-experimental comparison' for the two approaches and listed some of their respective advantages and handicaps. For example, he noted that similar size-corrected fecundity between once-mated and multiply-mated groups in a non-experimental comparison need not imply no advantage to multiple mating because larger (more fecund) females may have a higher 'necessity' to remate than small ones to achieve their potential fecundity. Indeed, in several species larger females exhibit a higher propensity to remate than do smaller females (e.g. Miyahara 1978; Torres-Vila et al. 1997; Bergström et al. 2002).

In general, a descriptive approach does not allow a causal relationship between polyandry and increased fecundity to be inferred. Consequently, Arnqvist and Nilsson (2000) excluded from their meta-analysis of the benefits of polyandry any studies in which a non-experimental, descriptive approach was used. This decision may, however, hide a potential pitfall because, as shown here, the descriptive method is more often used when studying species where females are mainly monandrous. So, by excluding descriptive studies, Arnqvist and Nilsson's (2000) meta-analysis is biased towards species that show higher natural levels of polyandry. Indeed, at least for lepidopterans, their meta-analysis excluded all predominantly monandrous species, and the same is also true of Vahed's (1998) narrative review. Although we found no significant difference in effect size between monandrous and polyandrous species when the experi-

mental method was used, our sample size was very small (n=4,18) so it is premature to conclude that there is no difference.

We suggest that a basic conceptual issue is whether we wish to calculate the effect of remating on fecundity for the average female, or whether we wish to test whether individual females mate multiply because it is to their benefit? The answer to this question, in combination with information on the extent to which females in a given species are likely to mate multiply when given the opportunity to control their mating rate, will influence the extent to which an experimental or descriptive method is more appropriate. We illustrate this by noting how an experimental comparison makes assumptions about the question being asked which can partly explain why differences in the reported effect of remating on reproductive output might systematically depend on the species' mating pattern.

In an experimental study, two groups of randomly chosen females with different mating history (multiply-mated or once-mated) are created. Each group consists, however, of a mixture of female phenotypes that may have very different propensities to mate multiply (Torres-Vila et al. 2001, 2002; Wedell et al. 2002). Females assigned to the multiple-mating group include not only naturally polyandrous females but also females that naturally *choose* to be monandrous. The single-mating group includes some females *forced* to be monandrous as well as those that would naturally *choose* to be monandrous. Because females are randomly assigned to groups, the proportion of females that are naturally monandrous should be the same in both groups. If individual females vary in their optimal mating rate, the estimated polyandry-fecundity relationship will be greatly influenced by the mating pattern of the target species because this will covary with the proportion of females that are naturally monandrous. For instance, in monandrous species fecundity differences between multiply-mated and once-mated females will be diluted because a high proportion of females that naturally choose monandry are assigned to the multiply-mated group where they obtain no benefit from remating. It also follows that the experimental method is more likely to detect a benefit of multiple mating in a polyandrous target species because a greater proportion of females assigned to the single-mating group are naturally polyandrous.

Ironically, this variation among females may also create a methodological problem in experimental studies by generating an unintended sampling bias that makes these studies quasi-experimental. If naturally monandrous females assigned to the multiple-mated group refuse to mate multiply they are usually excluded from the analysis, while all naturally monandrous females within the once-mated group are obviously included. This creates a systematic bias in the composition of the two groups. This alone will lead to fecundity differences between the groups if the fecundity of naturally monandrous and once-mated polyandrous females differs. One possible solution to this problem is to use only naturally polyandrous females by removing from both mating groups all females that show no post-mating receptivity (as a measure of natural monandry). However, in so doing, the conceptual question then becomes 'What is the effect of remating for naturally polyandrous females?' not 'What is the effect of remating for the average female?' Fortunately, in polyandrous species this bias is likely to be small because few females are naturally monandrous.

In conclusion, if fecundity differs significantly between naturally monandrous females and once-mated, naturally polyandrous females then the test method employed could dramatically bias results because both female types occur in the single-mating experimental group (see also Svärd and McNeil 1994) but the ratio will vary depending on the level of polyandry in the study species. The limited available evidence from primary research suggests that differences in the fecundity of monandrous and once-mated polyandrous females do occur, but may also be related to the species' mating pattern. In polyandrous species like *Earias insulana*, *Plodia interpunctella* and *Pieris napi*, the fecundity of monandrous and once-mated polyandrous females does not differ significantly (Tamhankar 1995; Cook 1999; Bergström and Wiklund 2002), but in *Choristoneura fumiferana* fecundity seems to be higher in monandrous than once-mated polyandrous females for some male larval diet regimes (Delisle and Hardy 1997). In the monandrous moth *Lobesia botrana*, fecundity is significantly higher in monandrous than in once-mated polyandrous females (Torres-Vila et al., unpublished data). Clearly, more work is required in which data is collected on the propensity of females to remate, rather than simply the number of times they do mate.

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