

# Experimental Evidence for Male Sequential Mate Preference in a Lekking Species

Noam Y. Werner & Arnon Lotem

Department of Zoology, Tel-Aviv University, Tel-Aviv, Israel

## Correspondence

Noam Y. Werner, The Tisch Family Zoological Gardens in Jerusalem, PO Box 898, Jerusalem 91008, Israel.

E-mail: wernerny@jerusalemzoo.org.il

Received: June 8, 2005

Initial acceptance: August 14, 2005

Final acceptance: October 23, 2005

(L. Sundström)

doi: 10.1111/j.1439-0310.2006.01202.x

## Abstract

In lekking species females visit male aggregations solely to copulate or have their eggs fertilized. Because lekking males do not contribute to parental care, evolutionary theory does not expect them to be choosy. However, we show here that in the cichlid fish *Astatotilapia flavijosephi* the lekking males exhibit sequential mate preference that strongly suggests a trade-off between present and future reproductive effort. We tested mate preferences of *A. flavijosephi* males by sequentially presenting them with two images of a gravid female, differing only in size. Previously, males were shown to prefer larger, more fecund females in simultaneous preference tests. The sequential presentation experiment reported here indicates that even in the absence of simultaneous presentation, males spent more time courting larger female images, and stayed longer in their vicinity. Thus, our study suggests that lekking males may be much choosier than previously appreciated. Furthermore, considering the intense competition among lekking males we also suggest that male choosiness, combined with other factors, may help to solve the 'paradox of the lek'. It can make less attractive females more available to subordinate males, thereby increasing the contribution of the latter to the population gene pool and keeping genetic variability among males at a level that justifies female choice.

## Introduction

In a wide variety of animal taxa females visit male aggregations or leks, solely to copulate and/or to have their eggs fertilized (Kirkpatrick & Ryan 1991). As lekking males do not contribute to parental care after copulation, evolutionary theory does not expect them to be selective, but rather to mate indiscriminately with as many females as possible (Trivers 1972). Indeed, as predicted by Trivers (1972), previous work on mate choice and mate preference has shown that males in non-lekking species can be as selective as females only when they contribute to parental care (Berglund et al. 1986; Jones & Hunter 1993; Johnstone et al. 1996; Kraak & Bakker 1998). Nonetheless, in lekking males preference or choice may still be expected, and indeed has recently been

found, when the males have to choose between two females simultaneously available to them (Sæther et al. 2001; Werner & Lotem 2003). However, there has been no evidence that lekking males vary their courtship efforts in relation to the level of attractiveness of females presented to them sequentially.

The importance of sequential mate preference has been suggested by several theoretical studies, which pointed out that in many species individuals are likely to encounter optional mates sequentially rather than simultaneously (reviewed by Gibson & Langen 1996). In contrast with simultaneous preference, during sequential preference individuals do not view all the possible mates at the same time but one after the other. In order to practice such sequential preference males should occasionally forego present mating opportunities in favour of potential

future ones. For males, such a trade-off between present and future reproductive effort is expected when reproduction is costly and therefore limits the number of copulations that an individual can afford (Galvani & Johnstone 1998). By analogy with optimal foraging theory (e.g. Stephens & Krebs 1986), such males resemble a group of individuals that search for prey items in a field and find them sequentially. Intuitively, if the costs of handling and ingesting the prey are low, individuals should pick up all prey items, irrespective of their size or quality. However, if handling or ingesting a particular prey can diminish the success of utilizing future prey, then individuals should trade-off present prey for potential future one and become selective. Applying this reasoning for male mate choice, we predict that sequential mate preference will occur when mating is costly, and may not occur when the cost of mating is negligible. In lekking species, where male reproductive investment is seemingly small and competition for females is intense, males are usually expected to mate with as many females as possible and, therefore, trading off present mating for potential future ones would appear unnecessary. However, although reproductive output of lekking males is not limited by parental care, their sperm supply and energy reserves are not infinite (e.g. Dewsbury 1982; Vehrencamp et al. 1989). In this case, lekking males may choose to allocate differential quantities of courtship effort or sperm to different females, according to the expected benefits. Such differential allocation may depend on male status, female quality, or the relative number of males and females on the lek (Galvani & Johnstone 1998).

In accordance with the predictions mentioned above, indirect evidence for sequential mate preference by lekking males was suggested by our recent study of the lek breeding cichlid *Astatotilapia flavijosephi* (Werner & Lotem 2003). *A. flavijosephi*, as other *Astatotilapia* species, breeds in leks, which are visited by female schools and characterized by frequent male–female interactions (N. Werner, unpublished data; Kirchshofer 1953; Fernald & Hirata 1977). The males occupy the lek for a lengthy period of time during which females that vary in size and fecundity may visit their territory (N. Werner, unpublished data). In this situation, sequential male mate preference may be expected, and indeed, was hinted by our previous study (Werner & Lotem 2003). We found that male courtship effort was higher in experiments involving larger, more fecund females. This finding prompted us to test experimentally the possibility of sequential mate prefer-

ence by lekking males. Here we report the results of a laboratory experiment in which we sequentially presented female images, which differed only in size, to wild caught *A. flavijosephi* males.

## Materials and Methods

### Study Species

*Astatotilapia flavijosephi* is an endemic species to Israel. It is locally abundant, mostly inhabiting rocky and densely vegetated areas in Lake Kinneret (the Sea of Galilee), the central part of the Jordan River and the numerous springs, pools, streams and canals that are connected with it (Goren & Ortal 1999). It is most closely related to central African haplochromine cichlids such as *Astatotilapia burtoni* (Werner & Mokady 2004) and shows similar behaviour (N. Werner, unpublished data). During the breeding season males aggregate in a certain area (i.e. a lek), defend small individual territories, 30–170 cm apart, and court passing females, which are often found in schools near the lek, at rates of two to 10 times per 5 min (see also Fernald & Hirata 1977 and Kirchshofer 1953 for details of *A. burtoni* and *Astatotilapia desfontainesi* behaviour in the field respectively). Courtship behaviour of *A. flavijosephi* resembles that of other haplochromine cichlids (McElroy & Kornfield 1990), which often includes energetically costly displays such as vigorous shaking in front of the female.

### Subjects

All experimental males ( $n = 14$ ) were wild caught (Nahal HaKibbutzim, Beit-She'an Valley, Israel). Prior to the experiments males were kept in individual 45-l aquaria in order to prevent the occurrence of intrasexual aggression, under a 13L:11D regime at approx. 28°C, and fed commercial cichlid pellets. Housing conditions and all experimental manipulations conformed to the institutional animal care and use committee standards and practices and were authorized by it.

### Female Images

The female images were created from a photo of one gravid female. Using Microsoft PowerPoint program the photo was slightly enlarged to create the 'large' female image (70 mm SL) and slightly reduced to create the 'small' female image (50 mm SL). Hence, the two images were identical except for size. These

two sizes are well within the natural size range of breeding *A. flavijosephi* females. A 50-mm long females weighed approx. 4 g (N. Werner, unpublished data), which is still larger than the smallest brooding female (1.9 g) observed in our study (Werner & Lotem 2003). The size of the larger image, 70 mm, is equivalent to a female that weighs approx. 11 g (N. Werner, unpublished data), and is still far from the largest females in this species (the largest female that was measured in our population was 84-mm long and weighed 17.8 g). As length/weight association is variable we chose a size difference that clearly represents females of different weights on top of lengths.

The photos were printed on transparent film (overhead) by a colour laser printer, and thin white plastic, cut to fit the images, was glued to their backs in order to make them opaque.

### Experimental Setup

A 145-l aquarium (180-cm long × 25-cm wide × 30-cm high) was divided into three compartments by transparent Perspex barriers. All compartments were fitted with a heater, an air stone, a water filter and with halved flowerpots that served as shelters. For each trial a male was placed in the middle compartment (70-cm long) and female images were placed next to the barriers in each side compartment (the large female image at one side and the small one at the other side, randomized over different experimental trials). The males were introduced into the experimental aquarium for a minimum of 18 h prior to the experiment for habituation, during which visual contact between the males and the stimuli was prevented by opaque barriers. The experiment began by removing the opaque barrier at one side of the test aquarium, thus allowing visual contact between the male and one of the female images. After 45 min the barrier was put back and the barrier at the other side of the test aquarium was removed, allowing visual contact with the second female image. Male behaviour during the experiment was videotaped using a 'Sony' (Sony, Tokyo, Japan) 8 mm camcorder.

To account for possible order or time effects each male was exposed to two different experimental treatments: during one treatment the large female image was presented first and during the other the small female image was presented first. Each male was given an interval of at least 4 wk between the two treatments. The order of treatments was assigned randomly, testing half of the males with

large–small treatment first, and the other half with small–large treatment first. Note that this experimental procedure was not designed for testing order effect per se (for which sequential testing with images of the same size is necessary), but merely to control for order of presentation as a possible confounding variable when testing size preference.

After the behavioural tests, each male was measured for standard length (to the nearest 0.5 mm, using callipers) and weight (to the nearest 0.1 g, using electrical balance), and a body condition index was calculated as weight/length ratio (weight/SL<sup>3</sup>; see Bolger & Connolly 1989). For each male we also counted the number of egg spots on its anal fin. These colourful spots, typical to male haplochromine cichlids, are thought to be involved in female choice and may be related to the male's sexual attractiveness (Wickler 1962; Hert 1989, 1991). To assess whether male choosiness may be related to its size, or to some other aspects of its quality, the above measurements were considered as possible covariates in the statistical analysis (see below).

### Video Analysis

For each test 10 min of videotape were analysed. Analysis started only after the male approached the female image. Two parameters were quantified: time spent near the female images (10 cm from the barrier or less), and time that males actively courted the female images (identified by 'quivering' behaviour, see above). Although courting is usually performed near the females, in order to avoid overlap between the two parameters time of active courting was not included in the parameter 'time spent near'.

### Statistical Analysis

We used SAS system for mixed models (Littell et al. 1996; using SAS software version 8.1) to construct the appropriate mixed models with female size (large vs. small) as a fixed effect, individual male as a random effect, and male's measurements of standard length, weight, body condition and number of egg spots as possible covariates. We first ran the models with all covariates and then used backward elimination to remove non-significant terms. The dependent variable for each analysis was either 'time spent near' or 'time spent courting', averaged over the two tests of a male with an image of a given size (i.e. the  $\bar{x}$  response to large or small in the two treatments – large–small and small–large). A class variable named 'order' was included in the models to distinguish

between males tested first with large–small treatment and those tested first with small–large treatment.

To further examine whether an order effect may be indicated in our data we compared the magnitude of size preference within each treatment (i.e. time spent near the large image minus time spent near the small image) between the large–small and small–large treatments. An order effect is expected to amplify the effect of size in one treatment and to attenuate it in the other. For example, a preference for ‘large’ and ‘first’ should amplify size effect in the large–small treatment and attenuate size effect in the small–large treatment.

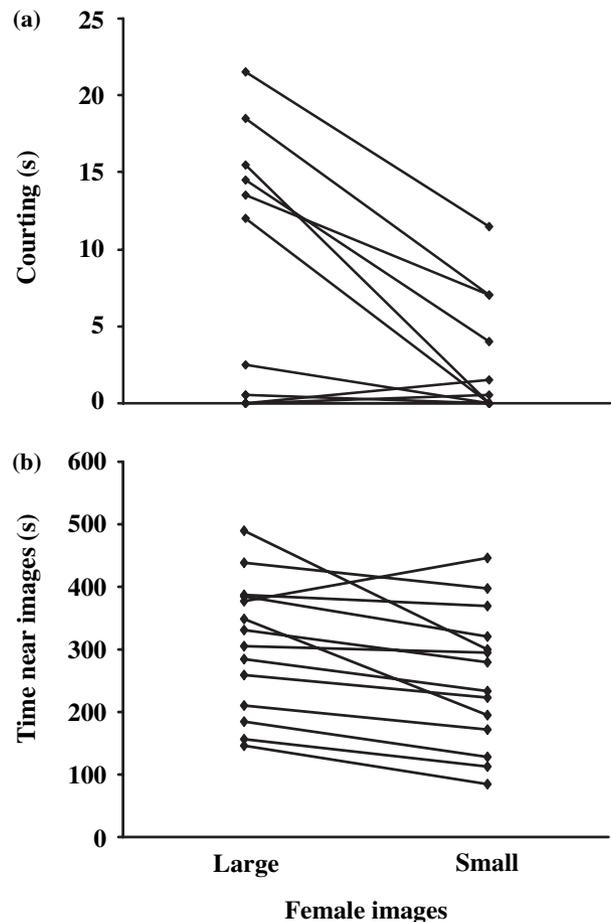
Three males that did not perform any active courting were removed from the analysis of ‘time spent courting’ but remained in the analysis of ‘time spent near’ (the results were the same also when these males were removed from the ‘time spent near’ analysis). Size measurements were missing for one male, reducing our sample size for testing the effect of covariates to 13 males.

## Results

Males spent more time courting larger female images, and stayed longer in their vicinity (Fig. 1). This effect was significant for both time spent near and time spent courting [( $F_{1,12} = 9.86$ ,  $p < 0.01$ ) ( $F_{1,9} = 10.39$ ,  $p = 0.01$ ) respectively; mixed model with size, order, and size  $\times$  order interaction as fixed effects, and individual as a random effect]. In neither analysis was the term ‘order’ and its interaction with size significant ( $F_{1,7} = 0.09$ ,  $p = 0.77$ ;  $F_{1,12} = 0.13$ ,  $p = 0.72$ , for time spent near and  $F_{1,5} = 0.66$ ,  $p = 0.45$ ;  $F_{1,9} = 0.07$ ,  $p = 0.79$  for time spent courting), suggesting that male behaviour was not affected by the order at which large and small females were presented.

None of the covariates included in the analysis were significant (see Table 1). To be extra cautious, we further fitted separately into the model each of the covariates and its interaction with female image size but also in this case none were significant. Therefore, it would appear that male level of choosiness was not related to male size, mass, body condition or the number of egg spots. Finally, we also tested the effect of size when all the four non-significant covariates were included in the model and it remained significant ( $F_{1,11} = 7.94$ ,  $p = 0.017$ ;  $F_{1,9} = 10.39$ ,  $p = 0.01$ , for time spent near and time spent courting respectively).

Overall, males behaved similarly in the first and the second tests and did not differ in the time they



**Fig. 1:** Male mate preference in the lekking haplochromine cichlid fish *Astatotilapia flavijosephi*. (a) The  $\bar{x}$  time (over the two tests) that each male invested in active courting when facing the large female image and when facing the small female image. (b) The  $\bar{x}$  time (over the two tests) that each male spent near the large female image and near the small female image

spent near the images ( $\bar{x} \pm \text{SE}$ :  $277.2 \pm 29.7$  and  $284.6 \pm 31.1$  respectively; Paired sampled t-test:  $t = 0.28$ ,  $n = 14$ ,  $p = 0.77$ ), or in the time they spent courting the images ( $\bar{x} \pm \text{SE}$ :  $6.6 \pm 2.3$  and  $2.7 \pm 1.2$  respectively; Wilcoxon matched pairs test:  $t = 15$ ,  $n = 14$ ,  $p > 0.1$ ). Differences in size preference within each treatment (time spent near the large image minus time spent near the small image) were similar for large–small and small–large treatment ( $\bar{x} \pm \text{SE}$ :  $45.6 \pm 33.4$  and  $60.43 \pm 27.1$  respectively; Paired sampled t-test:  $t = 0.29$ ,  $n = 14$ ,  $p = 0.77$ ), showing no indication that the order of presentation influenced male behaviour in our experiment. However, as mentioned earlier, because the experiment was not designed for testing order effect per se, we cannot rule out the possibility that an order effect may be expressed in *A. flavijosephi*

**Table 1:** Statistics for the four male traits that were included as possible covariates in the statistical analysis (see Results)

	Standard length (cm)	Weight (g)	Body condition	Number of egg-spots
$\bar{x}$	8.32	19.94	2.02	8.07
SD	1.33	12.28	0.20	3.28
Range	6.9–11	7.6–50.7	1.54–2.3	5–16
Analysis of time spent near the image	$F_{1,7} = 0.22, p = 0.66$	$F_{1,7} = 0.55, p = 0.48$	$F_{1,7} = 0.58, p = 0.47$	$F_{1,7} = 2.10, p = 0.19$
Analysis of time spent courting	$F_{1,5} = 0.01, p = 0.92$	$F_{1,5} = 0.04, p = 0.85$	$F_{1,5} = 0.26, p = 0.31$	$F_{1,5} = 0.29, p = 0.61$

under different circumstances, for example, when facing sequential choice between females of an equal size.

## Discussion

Our results show that *A. flavijosephi* males vary their mating effort in relation to the attractiveness of female images presented to them sequentially. The males spent more time near the large female image and courted more when facing the large female image, although they did not have another female image for comparison. To the best of our knowledge this is the first time that sequential male mate preference has been demonstrated in a lekking species.

The use of static images or dummies to study visual cues in fish behaviour allows a high degree of control of the tested parameter (see Rowland 1999 for a review). In our study the use of images that differed only in size excluded the possibility that male preference could be biased by female behaviour or by features that may be associated with female size in nature. The possible disadvantage of using an artificial stimulus is that it might not elicit as strong a response as live stimuli would (e.g. Balshine-Earn & Lotem 1998). However, while this problem may confound existing differences, it is unlikely to create differences that do not exist in nature. Moreover, the level of male response to the images in our experiment was not much lower than towards real females in our previous work (compare Fig. 1 in Werner & Lotem 2003 with Fig. 1 in the present paper). Another possible bias that should be considered is that males perceived larger images as closer in proximity and, therefore, interpreted them as more receptive females. We find this possibility unlikely, however, because studies on perceptual constancies in lower vertebrates suggest that fish possess mechanisms for size constancy (see Ingle 1998 for a review), which should thus have allowed males in our experiment to perceive the images as different in size rather than in distance. Furthermore, our experimental setup enabled males to move forward and nearly touch the images. This too should have

given them clear information on distance, which can easily be used to calibrate for size uncertainty (Walsh & Kulikowski 1998).

In many lekking species, display rate has been shown to correlate with male reproductive success (reviewed by Fiske et al. 1998). Thus, considering the highly competitive environment of a lek, a temporal reduction in male display rate or courtship effort may result in lost mating opportunities. Under these circumstances, it is easy to see that if courtship was cost free, the only evolutionary stable strategy among males should have been to court all females at maximal levels, irrespective of their size or receptiveness. In contrast, the implication of sequential mate preference of the kind shown by our study is that males court at less than their maximal levels when facing smaller females. Such reduced mating efforts can only make adaptive sense if courtship carries some costs that can outweigh the risk of losing a mate through male–male competition. In other words, a reduction in courtship efforts may only be justified if it can conserve resources that will improve future reproductive success.

There are several possible costs to courtship and mating behaviours that can possibly justify male selectivity. Sperm supply and energy reserves of lekking males are not infinite (e.g. Dewsbury 1982; Vehrencamp et al. 1989). Also time constraints or the risk of predation can incur costs on courtship or mating behaviours. Galvani & Johnstone (1998), for example, suggested that in the presence of detectable variation in female quality selective allocation of sperm may be adaptive. We suggest that sperm production represents only one aspect of the male time–energy budget. Accordingly, males may selectively allocate not only sperm but also courtship effort in general.

In the wild, *A. flavijosephi* leks seem to be very competitive places. Males defend small, individual territories (30–170 cm apart) and during all activity hours (light hours) females pass through or near these territories, which suggests that males are frequently faced with the need to assess females sequentially, as in our laboratory experiment. The

males interact with some of the females that pass in or near their territories at a rate of two to 10 times per 5 min, a rate which is similar to that is presented by other haplochromine species (N. Werner, unpublished data; Kirchshofer 1953; Fernald & Hirata 1977). It should also be noted that a female passing through the lek might be courted simultaneously by several males. This multiple male courting can potentially complicate male behavioural decisions and should be studied further. On the one hand, it could result in competitive escalation, making each male investing more in the present female. On the other hand, escalation may not be adaptive in all cases. For example, in the case of a small, less attractive female, it might be better for a dominant male to save its efforts rather than to increase it. In our experimental set up each male was tested in isolation in order to test the mere presence of sequential mate preference in this species. To test how male-male competition interacts with male sequential preference, further experimental work is necessary.

This study shows that in lekking species males may be more discriminating than previously appreciated. Based on these results we suggest that male preference in leks has an interesting implication that deserves further attention, because it might help to solve the so-called 'paradox of the lek'. This paradox argues that strong female choice for males with 'good genes' is expected to reduce the genetic variability among lekking males to a level that will make female choice unprofitable (i.e. a small cost of the choice mechanism will offset its benefit). Several ideas have been suggested to explain the maintenance of female choice in lekking species (e.g. Pomiankowski & Møller 1995; Rowe & Houle 1996; Randerson et al. 2000). However, we suggest that male mate preference too can further contribute to the resolution of the paradox. Male mate preference may result in making less attractive females more available to subordinate males, thereby increasing the latter's contribution to the population gene pool. Under these circumstances, this contribution of genes may maintain genetic variability among males at a level that will justify female choice even in a lekking species.

### Acknowledgements

The authors wish to thank L. Stone and J. Norman for comments, an anonymous referees and the associate Editor, Lotta Sundström, for helpful suggestions, A. Cohen and E. Dove for statistical advice and N. Sharon for technical assistance. This research

was supported by an Israel Science Foundation grant (grant no. 681/96-17.2) to A.L. and a George S. Wise Faculty of Life Sciences PhD scholarship to N.Y.W. The experiments reported here comply with the current laws and ethical guidelines of the country in which they were performed.

### Literature Cited

- Balshine-Earn, S. & Lotem, A. 1998: Experimental evidence for individual recognition from video playbacks in a cooperatively breeding cichlid (*Neolamprologus brichardi*). *Behaviour* **135**, 1–18.
- Berglund, A., Rosenqvist, G. & Svensson, I. 1986: Mate choice, fecundity and sexual dimorphism in 2 pipefish species (Syngnathidae). *Behav. Ecol. Sociobiol.* **19**, 301–307.
- Bolger, T. & Connolly, P. L. 1989: The selection of suitable indices for the measurement and analysis of fish condition. *J. Fish Biol.* **34**, 171–182.
- Dewsbury, D. A. 1982: Ejaculate cost and male choice. *Am. Nat.* **119**, 601–610.
- Fernald, R. D. & Hirata, N. R. 1977: Field study of *Haplochromis burtoni*: quantitative behavioural observations. *Anim. Behav.* **25**, 964–975.
- Fiske, P., Rintamaki, P. T. & Karvonen, E. 1998: Mating success in lekking males: a meta-analysis. *Behav. Ecol.* **9**, 328–338.
- Galvani, A. & Johnstone, R. A. 1998: Sperm allocation in an uncertain world. *Behav. Ecol. Sociobiol.* **44**, 161–168.
- Gibson, R. M. & Langen, T. A. 1996: How do animals choose their mates? *Trends Ecol. Evol.* **11**, 468–470.
- Goren, M. & Ortal, R. 1999: Biogeography, diversity and conservation of the inland water fish communities in Israel. *Biol. Conserv.* **89**, 1–9.
- Hert, E. 1989: The function of egg-spots in an African mouth-brooding cichlid fish. *Anim. Behav.* **37**, 726–732.
- Hert, E. 1991: Female choice based on egg-spots in *Pseudotropheus aurora* Burgess 1976, a rock dwelling cichlid of Lake Malawi, Africa. *J. Fish Biol.* **38**, 951–953.
- Ingle, D. 1998: Perceptual constancies in lower vertebrates. In: *Perceptual Constancy: Why Things Look as They Do* (Walsh, V. & Kulikowski, J., eds). Cambridge Univ. Press, New York, pp. 173–191.
- Johnstone, R. A., Reynolds, J. D. & Deutsch, J. C. 1996: Mutual mate choice and sex differences in choosiness. *Evolution* **50**, 1382–1391.
- Jones, I. L. & Hunter, F. M. 1993: Mutual sexual selection in a monogamous seabird. *Nature* **362**, 238–239.
- Kirchshofer, R. 1953: Aktionssystem des Maulbrüters *Haplochromis desfontainesii*. *Z. Tierpsychol.* **10**, 297–318.

- Kirkpatrick, M. & Ryan, M. J. 1991: The evolution of mating preferences and the paradox of the lek. *Nature* **350**, 33—38.
- Kraak, S. B. M. & Bakker, T. C. M. 1998: Mutual mate choice in sticklebacks: attractive males choose big females, which lay big eggs. *Anim. Behav.* **56**, 859—866.
- Littell, R. C., Milliken, G. A., Stroup, W. W. & Wolfinger, R. D. 1996: SAS System for Mixed Models. SAS Institute, Inc., Cary, NC.
- McElroy, D. M. & Kornfield, I. 1990: Sexual selection, reproductive behavior, and speciation in the mbuna species flock of Lake Nyasa (Pisces: Cichlidae). *Environ. Biol. Fishes* **28**, 273—284.
- Pomiankowski, A. & Møller, A. P. 1995: A resolution of the lek paradox. *Proc. R. Soc. Lond. B* **260**, 21—29.
- Randerson, J. P., Jiggins, F. M. & Hurst, L. D. 2000: Male killing can select for male mate choice: a novel solution to the paradox of the lek. *Proc. R. Soc. Lond. B* **267**, 867—874.
- Rowe, L. & Houle, D. 1996: The lek paradox and the capture of genetic variance by condition dependent traits. *Proc. R. Soc. Lond. B* **263**, 1415—1421.
- Rowland, W. J. 1999: Studying visual cues in fish behavior: a review of ethological techniques. *Environ. Biol. Fishes* **56**, 285—305.
- Sæther, S. A., Fiske, P. & Kålås, J. A. 2001: Male mate choice, sexual conflict and strategic allocation of copulations in a lekking bird. *Proc. R. Soc. Lond. B* **268**, 2097—2102.
- Stephens, D. W. & Krebs, J. R. 1986: *Foraging Theory*. Princeton Univ. Press, Princeton, NJ.
- Trivers, R. L. 1972: Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man, 1871—1971* (Campbell, B., ed.) Aldine-Atherton, Chicago, IL, pp. 136—179.
- Vehrencamp, S. L., Bradbury, J. W. & Gibson, R. M. 1989: The energetic cost of display in male sage grouse. *Anim. Behav.* **38**, 885—896.
- Walsh, V. & Kulikowski, J. 1998: *Perceptual Constancy: Why Things Look as They Do*. Cambridge Univ. Press, New York.
- Werner, N. Y. & Lotem, A. 2003: Choosy males in a haplochromine cichlid: first experimental evidence for male mate choice in a lekking species. *Anim. Behav.* **66**, 293—298.
- Werner, N. Y. & Mokady, O. 2004: Swimming out of Africa: mitochondrial DNA evidence for late Pliocene dispersal of a cichlid from Central Africa to the Levant. *Biol. J. Linn. Soc.* **82**, 103—109.
- Wickler, W. 1962: 'Egg-dummies' as natural releasers in mouth-brooding cichlid fish. *Nature* **194**, 1092—1094.