

## BRITISH ORNITHOLOGISTS' UNION

## 'Do-si-do your Partner': Report on the Annual Conference of the BOU

The 1993 Annual Conference was held at Losehill Hall, Derbyshire, from 26–28 March. About 70 delegates from 10 European countries participated, and it is difficult to say what attracted them most. Was it the theme of the conference *Reproductive competition: Extra-pair copulation (EPC) and intra-specific brood parasitism (ISB)*? Was it the good number of well-known speakers? Was it the nice and quiet conference site in a rural setting, or was it the field trip into Peak National Park? Whatever their reasons for coming, nobody left disappointed. Kate Lessells and Tim Birkhead had put together an excellent scientific and social programme which started with . . . a programme change. The planned opening talk by Tony Williams on "A total lack of reproductive competition in the Antarctic" had to be cancelled, because Tony's slides were still rolling on the ocean. Luckily, Tim Birkhead had plenty of slides—of course, exclusively on the existence rather than on the lack of reproductive competition. He used them to rush us through some of the main topics we could expect during the conference and then sent us to the bar.

Most of the 17 talks during the next 2 days fell into one or more of the following groups: 1) the extent of EPCs and ISB as detected through DNA-fingerprinting techniques, 2) determinants of EPCs and ISB, 3) counter measures and responses to EPCs and ISB.

1) DNA-fingerprinting techniques. These techniques for analysing parentage now seem to be as routinely applied to studies of avian reproduction as are Chi-square tests in statistics. In fact, fingerprinting was probably more often mentioned than statistical tests. A closer look, however, shows that all analyses come from a few expert laboratories, most of them from the one of Terry Burke. No wonder, that Terry knows "DNA fingerprinting reveals all"; this was the title of his talk. He started with a brief introduction into various new techniques, contrasted the advantages and disadvantages of multi-locus v single-locus probes and reported about some very recent developments, including a single-locus probe which works for a large number of Passerines. He then presented some results from various species which showed that the extent of EPCs may differ even in species with similar biology such as the lekking Black Grouse *Tetrao urogallus* and Ruff *Philomachus pugnax*. Mike Siva-Jothy reminded us, in a stimulating talk, that the idea of sperm competition originated from studies in insects, where investigation of the structure of reproductive tracts has given a lot of insight into the various mechanisms of reproductive competition within the female body. Some of these mechanisms are also relevant for birds, e.g. sperm replacement, sperm removal and frequent copulations to keep sperm in priority areas.

The subsequent talks revealed that proportions of EPCs

in birds range widely from zero or very low, as in Dik Heg's study of Oystercatchers *Haematopus ostralegus* where only 1 out of 63 chicks (=1.5%) was an extra-pair young (EPY), through moderate proportions as in Bart Kempenaers' study of Great Tits (10–14% EPY) to the high levels of the Reed Bunting *Emberiza schoeniclus*. In this species, Andrew Dixon and Sean O'Malley found that reproductive success from their own nest was achieved by only about 50% of the males. EPCs account for more than 50% of all young and affect 70–90% of the nests. In this case, and in several others, behavioural observations of copulations underestimate the number of EPY, which illustrates the power of DNA-fingerprinting techniques. With respect to ISB, behavioural and genetical data usually agree better, as Kate Lessells and Benoit Lequette demonstrated for European Bee-eaters *Merops apiaster*. When comparing nest parasitism rates calculated from fingerprints with those calculated from the appearance of two eggs during the same day, they found 3.5% and 2.6%, respectively.

In most species ISB rates are much rarer than EPC rates, but in moorhens it is the other way round. In a series of experiments, Susan McRae investigated why the hosts accept dumped eggs and came up with two explanations which are not mutually exclusive. First, the costs of rejection through desertion outweigh the costs of raising a few more parasitic young. Second, mothers and daughters sometimes lay into the same nest, and fathers and sons are often neighbours; thus, kin benefits seem to lower the costs of being parasitized. She could exclude the possibilities that hosts are not aware of the parasitism and that host males had copulated with the parasitising female, a situation referred to as "quasi-parasitism". Such quasi-parasitism, however, was fairly frequent in Maria Alvez's study on Sand Martins *Riparia riparia* where it affected 17% of the nests and 7% of the chicks.

2) Determinants of EPCs and ISB. Studies on the factors determining EPCs and ISB focussed on morphological and behavioural differences among individuals. More and more evidence is accumulating that males with higher age, better body condition, longer tarsi, larger badges, longer tail feathers and higher song rates seem to achieve more EPCs than others. This is the overall message from the studies of Andrew Dixon (Reed Bunting), Bart Kempenaers (Great Tits *Parus major*), Sean O'Malley (Reed Bunting), Jon Wetton (House Sparrows *Passer domesticus*) and from Anders Moeller's review on "Sperm competition and sexual selection" which incorporated his own studies on House Sparrows and Swallows *Hirundo rustica*. The reasons for these differences in reproductive success differ. In some species females seem to be in control of EPCs and actively choose superior males, e.g. by intruding into their territories when fertile (Blue Tit

*Parus caeruleus*). In other species superior males may be more active in attempting to copulate with other females or may outcompete their rivals (e.g. in communal displays of House Sparrows). Within this framework, Fiona Hunter challenged the standard explanation that males compete and females choose. She suggested that in species where both sexes invest heavily in the brood, both should compete and choose. Her experiments with models of Crested Auklets *Aethia cristatella* confirmed that indeed both sexes choose. Whether females are also competing for EPCs with good quality males still needs to be tested. The tendency to engage in EPCs will differ among individuals as pointed out by Anders Moeller. The later in the season a female mates, the lower the quality of available males, but the higher her chances for multiple matings. This idea, that the mismatch between the partner quality which an individual wants and the one it gets is important, was also developed by Marion Petrie to explain the large variation in copulation frequency which is observed in pairs of the same species.

Where reproductive success cannot be related to individual traits, as in Jarmo Piironen's study of Whinchats *Saxicola rubetra*, this may have several reasons. One is, as Andrew Dixon pointed out, that the relevant measure for quality is often difficult to define. What matters for fitness? Song or plumage? Size or colour of a badge? Wing or tarsus length? Another reason is that choice is restricted through time and space. Time constraints may act where a short season leads to high synchrony. Spatial constraints are clearly illustrated by two sets of data. First, the proportion of colonial species "present" at the conference was much higher than the proportion of colonial species in the avian world. This indicates that the absence of territory boundaries and the closeness of breeding pairs offers plenty of possibilities for EPCs and ISB. Second, in territorial species most EPCs and ISB come from neighbours.

3) Counter measures against and responses to EPCs and ISB. A frequent counter measure against EPCs is mate guarding. Its importance was illustrated by Helen Riley's "Confessions of House Martin [*Delichon urbica*]". Most EPY were from the last egg, due to the fact that males decrease their mate-guarding intensity before the end of the females' fertile period. Also, when males are removed, as in Maria Alvez's study of Sand Martins, EPCs increase. In species where guarding is less pronounced, males may ensure their paternity through high copulation rates (e.g. 40 times/day in House Sparrows). ISB is normally counteracted by removing the dumped egg from the nest, but only until the host female has started laying herself. Thereafter, rejection rates decrease as Susan McRae (Moorhens *Gallinula chloropus*) and Kate Lessells (Bee-eaters) have shown by adding artificial eggs at different times. This is a safeguard against throwing out own eggs, as is the fact that Bee-eater males never reject eggs, probably because they do not know when their own females have laid.

In terms of the response to EPCs no uniform pattern emerges. In pairs of Sand Martins and Dunnocks *Prunella*

*modularis*, copulations of a female with more than one male do not affect feeding rates; but in trios of Dunnocks they do, as Ben Hatchwell reported. For trios there exists a significant positive relationship between paternity and the amount of care which the beta male provides. Through removal experiments it could be shown that a beta male will only feed when it has achieved copulations during the egg-laying period. The difference in response between males in pairs and trios can be explained by assuming that the survival of the chicks is more at risk when one out of two individuals reduces its feeding than when one out of three does it. In the latter case two parents remain to compensate. The importance of compensation was also brought up in Jon Wright's talk about Starlings *Sturnus vulgaris*. He argued that cuckolded males should only reduce parental care when females either compensate or males gain in terms of future reproduction. By temporarily caging mated females close to caged males and their boxes, he tested how the females' partners reacted to their mates' "infidelity". After females were released, cuckolded males did neither increase their guarding, nor did they copulate more. They did, however, increase their song rate. This suggests that males gain more by attracting new mates than by guarding unfaithful ones.

This list is by no means complete. Most papers dealt with many more aspects than the one for which they have been cited above. I also did not mention the very interesting posters, mainly because the diversity of their topics would have made this report too long. Overall, the conference gave an excellent overview about what we presently know. It also clearly showed what we do not know. Probably most striking was the almost total lack of information about ecological determinants of reproductive competition. A few speakers mentioned that density seems to affect EPCs (e.g. in Great Tits and Reed Buntings), that nest site quality might explain differences in ISB (e.g. in House Sparrows) and that sex ratio, breeding synchrony and other environmental factors could influence the intensity of mate guarding (e.g. in Starlings). No study, however, tested ecological explanations of EPCs and ISB with the same rigour with which they tested the effects of individual traits. This is a gap in our understanding of reproductive competition that needs to be filled in the future.

Now to the social events. One event consisted of groupwise excursions into various areas of Peak National Park. These had been extremely well organized. Good weather had been ordered; when one of the excursion vehicles ran out of petrol it happened right in front of a gas station; a large number of tame red grouse had been placed in scenic sites close to the footpath and, after making it to the mountain top, members of at least one group were provided with refreshments. Kate Lessells had secretly carried them up the steep slopes. When Kate arrived as the last group member and a bit out of breath, she first found herself exposed to some mocking remarks about field work, but when she opened her rucksack and produced large numbers of Mars® bars and packets of fruit juice she immediately became the centre of attrac-

tion. Another clear proof that the "handicap principle" *does* work.

After returning from the excursions we ran right into the second social event. The poster session was opened with a wine reception by Academic Press/T & AD Poyser to launch Tim Birkhead's new book. The wine was there (and good), but the book was not ready (and therefore of unknown quality). This was unfortunate, but the reverse scenario (i.e. book present, wine absent) would have been even worse, especially as there were already so many books on display through the Natural History Book Service.

The third social event was a "Ceilidh", a typical scottish party. It consolidated the conference theme *Reproductive competition* by complementing the theory of the talks with practical exercises. Thanks to an extremely good band (not to be confused with bands in DNA-fingerprinting!) and sexy sounding dance titles like "Ladies' chain" or "Do-si-do your partner" both sexes immediately started displaying vigorously on a lek (=dance floor). By instructing people when to do which steps, the leader of the band desperately tried to make the whole display ritualized, if not stereotyped; but he failed. There was enormous variance in morphological

characters like tarsus length or brilliance of plumage, but also in loudness of voice, elegance of body movements and other behavioural traits on which selection could operate. It also turned out that there was no close correlation between various measures of quality. Some people who had performed very well on the intellectual stage appeared rather clumsy on the dance floor. Fortunately, the opposite was not true: there simply were no poor talks during the conference.

In summary, I do not know whether the BOU needs and wants more publicity for its annual conferences. After all, it is the relatively small number of participants which allows intensive discussions and provides good opportunities to establish new contacts and strengthen already existing ones. This, together with the high scientific quality of the presentations makes it an extremely attractive type of conference. For me it was the first BOU meeting, but it definitely will not be the last one. Therefore, I do not hesitate to highly recommend these conferences to anyone interested in ornithology.

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