Etología, 3:79-93 (1993)

Studying animal behaviour: what's the use?

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ABSTRACT. *Studying animal behaviour: what's the use?*.- It is not always easy to recognise the practical value of studies of animal behaviour especially those concerned with its functional significance. Using a range of examples, this paper reviews the practical value of studies of animal behaviour, particularly with respect to improving productivity of managed populations, pest control and conservation problems.

KEY WORDS. Animal behaviour, Practical value

Introduction

Scientific study of the behaviour of animals improves our understanding of the natural world, and as such is as valuable as the pursuit of knowledge in any pure science. Nonetheless, we are often called upon by government bodies, hard pressed funding agencies, or indeed by the general public, to demonstrate the practical spinoffs of ethological research. For work that is clearly geared towards solving problems relating to human or animal health or welfare (i.e. applied rather than pure science) this is relatively easy. For many other branches of ethology, it is not. Furthermore, to many scientists interested particularly in the adaptive significance of behaviour and in the development of an appropriate theoretical background, the largely descriptive and captive based context of much of 'applied ethology' is relatively unattractive. Yet much more ethological work can have practical spinoffs than appears at first sight, and the interaction between the development of theory and the solving of practical problems is, in practice, often a two-way process. In this brief review, using a selection of examples from a range of different contexts, I shall try to show that detailed research in animal behaviour, far from being an esoteric, self-indulgent pursuit, is extremely valuable to modern society.

What does ethology offer?

While some (non-ethologists!) claim that managing the behaviour of animals is largely common sense, a lack of scientific understanding of animal behaviour often results in pest control being

based on crude culling policies, populations being harvested in non-sustainable and inefficient ways, conservation strategies failing and animals being kept in poor conditions. Common sense is often nonsense. What ethology offers is the scientific method, involving the development of a sound theoretical framework generating testable hypotheses and predictions, and the collection of rigorous and reliable data coupled with sophisticated analysis of variation in the data. The kinds of animal problems to which ethologists can make significant contributions are many and varied, and can largely be grouped under the following headings: Improving Animal Health & Welfare, Improving Productivity, Pest Control and Conservation (see Monaghan, 1984; Metcalfe & Monaghan, 1987; Monaghan & Wood-Gush, 1990 for more detailed discussion). In this review I shall concentrate mainly on the last three, since other papers deal with the first.

Improving productivity

The management of many wild, as well as captive, animal populations is geared towards maximising productivity whether this be for the production of food or other resources, or for so-called sport. It is essential that the growth of individuals within the population is managed to provide an economic yield and, particularly with wild populations, that animals are harvested in a sustainable way. There is a considerable body of literature on the importance of behaviour in managing agricultural species (e.g. see Wood-Gush, 1990). However, management strategies employed for wild species often do not take into account the social behaviour of the animals and its functional significance, and the regimes employed may therefore fall short of their initial aims.

Populations of ungulates are managed in many areas for meat production and for sport shooting.

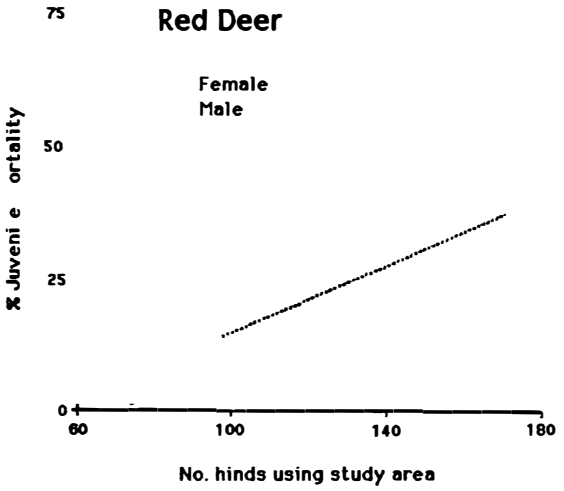

FIGURE 1. The change in juvenile mortality rate of male and female red deer in relation to population density, as indicated by the number of hinds using the area; male mortality is more severely affected than that of females. From Clutton-Brock & Albon, 1989.

[Cambio en la tasa de mortalidad de juveniles de ciervo machos y hembras en relación a la densidad de población, indicada por el número de hembras que usan el área; la mortalidad de los machos se ve afectada mas severamente que la de las hembras.]

The classic studies of Clutton-Brock and his co-workers on red deer *Cervus elaphus* on Rum, Scotland have made a very important contribution to the development of behavioural ecology; they also provide information which should overturn several traditional management practices. For example, red deer populations are maintained in sporting estates in many parts of Scotland, and the aim of management policies is usually to maximise the number of mature stags that can be shot by stalkers. To this end, the policy is usually to cull few if any hinds, based on the no doubt common sense belief that maximising the number of breeding females will maximise the rate at which male young are produced, hence maximising the number of mature stags. Moreover, it has been assumed that any

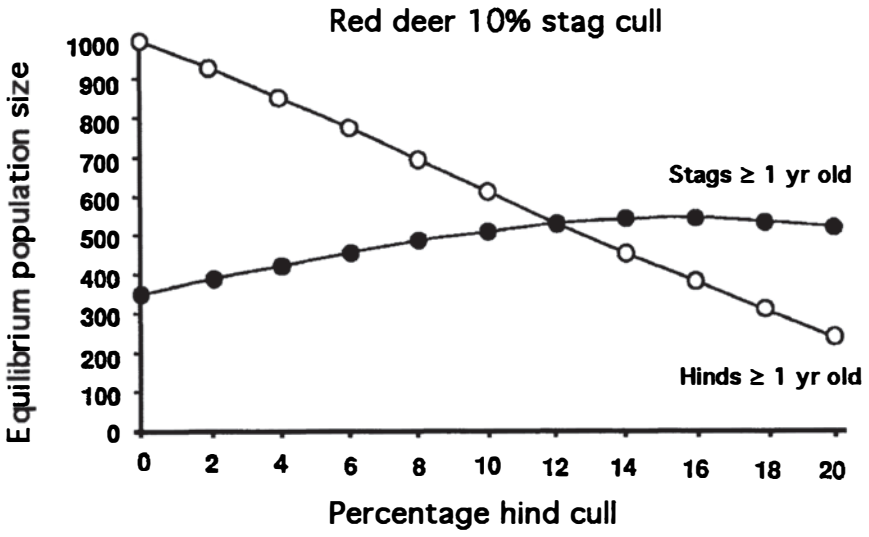

FIGURE 2. The calculated equilibrium population size of stags and hinds over one year old when 10% of stags are culled in relation to the percentage hind cull in red deer. Note that when no hinds are culled, hinds greatly outnumber stags; this is also the case when no stags or hinds are culled From Clutton-Brock & Lonergan in press.

[Ttamaño de la población en equilibrio de machos y hembras de ciervo, de un año de edad, calculado cuando el 10% de los machos se entresacan en relación al porcentaje de hembras entresacadas.]

excess females will not adversely affect the males, since the stags are larger and so will be able to outcompete the hinds at feeding sites if food is short. However, this takes no account of differences in the behavioural ecology and population dynamics of male and female red deer. Unculled populations show a marked female bias, with 1.5 to 2 females per male (Clutton-Brock & Albon, 1989). Males have higher metabolic requirements and they range more widely and are more susceptible to low temperatures and prolonged snow cover than females; there is also some evidence that females can exclude males from the best grazings in winter by reducing the height of the sward to levels at which males cannot economically feed on it (Clutton-Brock & Albon, 1989). As a consequence, male mortality is higher than that of females, since they are less able to withstand poor conditions in winter. The growth and survival of stags is more strongly affected by rising population density than that of hinds (fig. 1). Thus, as Clutton-Brock & Lonergan (in press) have recently demonstrated, maintaining a high population of hinds actually depresses male survival. Sporting estates, contrary to common-sense policy, need to cull hinds relatively heavily to maximise stag production (fig. 2).

A similar situation can arise with the management of wild fish stocks, such as those of the Atlantic salmon *Salmo salar*. Here the aim is to maximise the number of large adult fish that can be caught either in nets or by anglers. These fish are born in freshwater and then migrate to sea where most of their growth occurs before they return to their natal streams to spawn. The problem lies in the fact that males do not necessarily need to

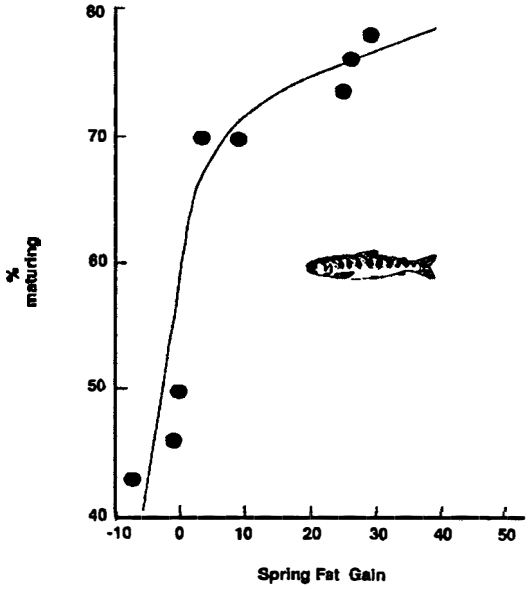

FIGURE 3. The percentage of male salmon becoming sexually mature while still at the freshwater stage (parr) November in relation to fat gain the previous spring; the more fat the fish gain, the more likely they are to mature at a very small size, having foregone the growth phase at sea altogether. From Rowe et al., 1991.

[Porcentaje de machos de *Salmo salar* que alcanzan la madurez sexual mientras aún permanecen en el estado de agua dulce.]

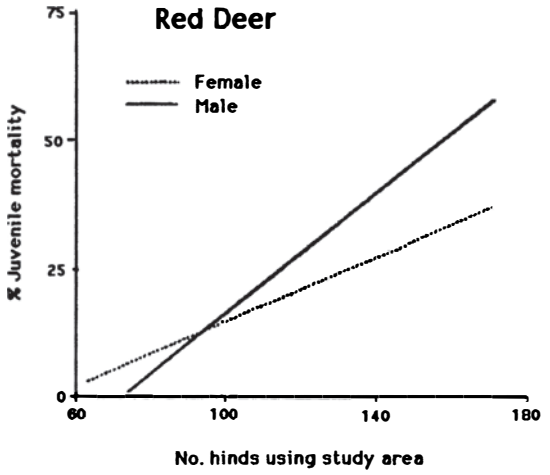

FIGURE 4. Upper graph - the decline in the number of juveniles migrating to sea at Lake Dalneye, Russia over a 40 year period. The decline is partly due to a decline in numbers caused by overfishing, and an increase in the % of males becoming sexually mature at the freshwater stage i.e. non-migratory 'sneakers', as shown in the lower graph. From Thorpe 1989.

[Gráfico superior, disminución en el número de juveniles que migran al mar en Lake Dalmeye, Russia en un periodo de 40 años. La reducción es debida a una merma de los efectivos causada por sobrepezca, y a un incremento en el porcentaje de machos que llegan a ser sexualmente maduros en el estado de agua dulce, es decir, de individuos no migrantes (Gráfico inferior).]

migrate to sea - they can omit this stage of the life-cycle and so become sexually mature at a relatively tiny size (20-40 g, approximately one hundredth the size of the 'proper' adults). The large migrant males obtain matings with females by aggressive competition, but the small non-migrant males adopt an alternative reproductive strategy of sneaking: often several sneakers will gather around a spawning pair of large adults and will dart in to release their sperm at the moment of egg deposition.

Males tend only to mature at a small size if they can accumulate the necessary energetic reserves (fig. 3); otherwise they will migrate. Thus an increase in individual growth rates tends to lead to an increase in the proportion of males that mature as small sneakers. While these sneakers can potentially migrate to sea after having been a sneaker (and so come back to breed again as a full-size male), relatively few of them will do so since the mortality rate of sneakers is quite high.

These alternative reproductive strategies have important consequences for the management of salmon populations. If conditions for the young fish

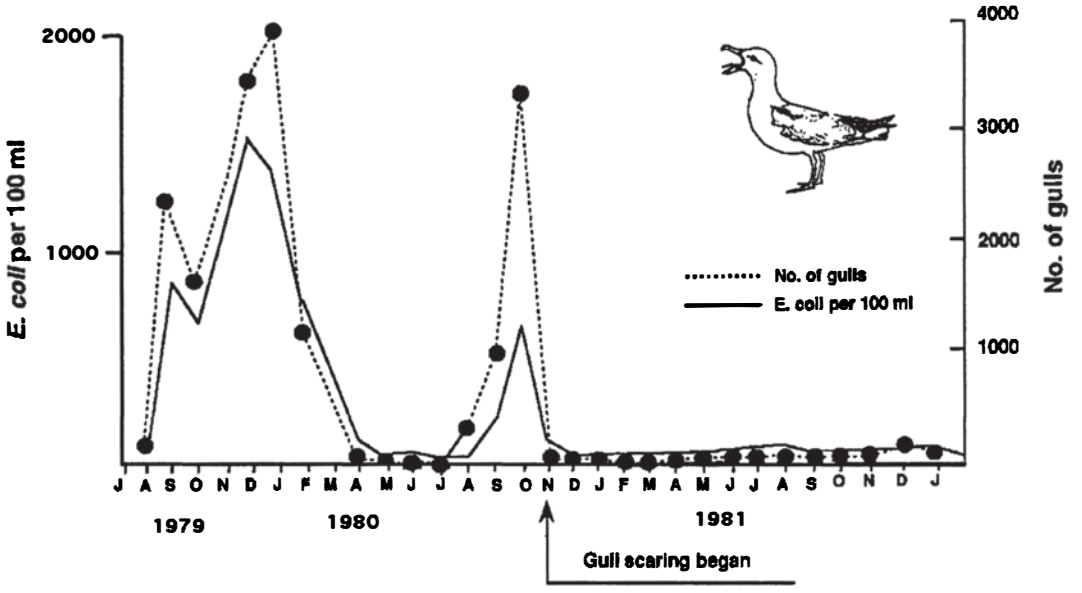

FIGURE 5. The relationship between the number of roosting gulls and the level of contamination (as indicated by *E. coli* levels) at a water storage reservoir near Glasgow. Deterring the gulls from roosting removed the contamination problem. From Benton et al., 1983.

[Relación entre el número de *Larus* spp. en el dormidero y el nivel de contaminación (indicado por los niveles de *E. coli*) en un embalse cerca de Glasgow. Impidiendo el descanso de las gaviotas se elimina el problema de contaminación.]

in the streams are too good, many males will mature as sneakers and so the number of fish that migrate to sea (and so reach a catchable size) will drop. This is illustrated graphically in a long-term data set from Lake Dalneye, Russia. Over-fishing caused a massive reduction in the density of young fish. This allowed faster growth rates, and so many more of the males matured as sneakers. As a consequence, the number of migrants dropped drastically due to (a) the initial overfishing causing a reduction in the size of the population and (b) many of the remaining males opting not to migrate (fig. 4). An understanding of these alternative reproductive strategies could have led to fishing regulations that maintained the population density at a level where males rarely opted to mature as sneakers.

Atlantic salmon also illustrate the fallacy of trying to maximise individual growth rates in order to produce an economic yield is also well illustrated by Atlantic salmon. These fish are reared commercially in fresh water and in sea cages in intensive aquaculture programmes that take little account of the social behaviour and life-history strategies of the fish (Metcalfe, 1990). The basic premise of farmers has tended to be that growth rates should always be maximised (since this will result in large fish in the shortest possible time). They have also tended to feed fish on high-energy foods over the winter, on the assumption that the fish

need more fat stores when it is cold. However, as described above, salmon (especially males) tend to mature early but at small sizes if their growth rates have been high and if they have built up their fat stores (fig. 3). The increased mortality rate, poorer growth and drop in flesh quality of maturing fish means that the farmer must market the fish once they start to mature. The decision over whether to mature or not appears to be made by young male salmon in late winter. Thus feeding salmon on high-fat diets at this time has precisely the opposite effect to that intended - it prompts the fish into maturing early, at below the size that is economically optimal. The best strategy for the farmer is the counter-intuitive one of restricting food intake during the winter, so causing the fish to deplete their fat reserves. This results in a smaller proportion of the fish maturing the following breeding season (fig. 3). It also has the added benefits of reducing feed costs and the pollution of the sea bed that results from uneaten food

Pest control

Behavioural studies can provide a range of effective alternatives to culling when dealing with agricultural pests (see Greig-Smith, 1990 and Inglis & Shepherd, 1990). This is also the case when dealing with pests in other contexts. For example, the large gulls (*Larus* spp.) can carry pathogens of man and domestic animals, picked up when scavenging on waste products (Monaghan et al., 1985). Therefore, when these birds roost overnight on water storage reservoirs, they can pose a considerable health risk and minimising this risk can involve expensive upgrading of water treatment plants or covering of storage reservoirs. The city of Glasgow was faced with such a problem in the early 1980's. Serious contamination at the major water reservoir was correlated with the number of roosting gulls (fig 5). By taking into account the high priority the birds attribute to a safe overnight roost and the existence of an alternative and acceptable roost site nearby, it was possible to use distress calls to effectively reduce the number of roosting birds (fig. 5), thereby allowing the city to defer the expenditure of an estimated 30 million pounds in upgrading the treatment plant (Benton et al., 1983). Such scaring however only works well in certain situations, and can actually exacerbate the problem when used at colonies after the birds have established territories; an understanding of the changing priorities and responses of the birds in different situations is essential if such methods are to be used effectively (Monaghan, 1984).

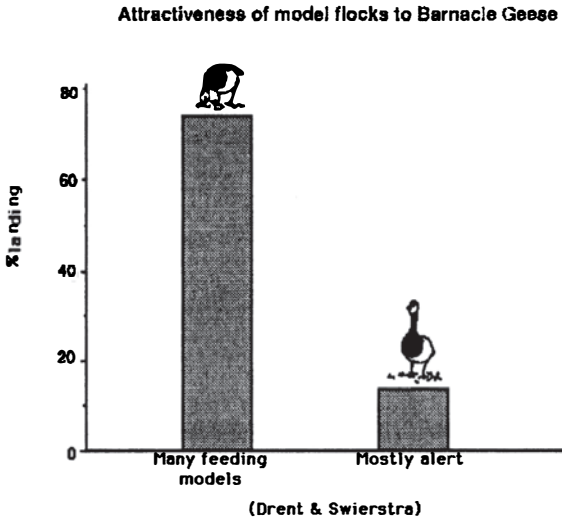

FIGURE 6. The effect of the posture of models on the attractiveness of model flocks to barnacle geese. Flocks with a high proportion of models in an alert posture were not very attractive. From Drent and Swierstra, 1977.

[Efecto de la postura de los modelos sobre la atracción de bandos modelo en *Branta leucopsis*. Los bandos con alta proporción de modelos en postura de alerta no fueron muy atractivos.]

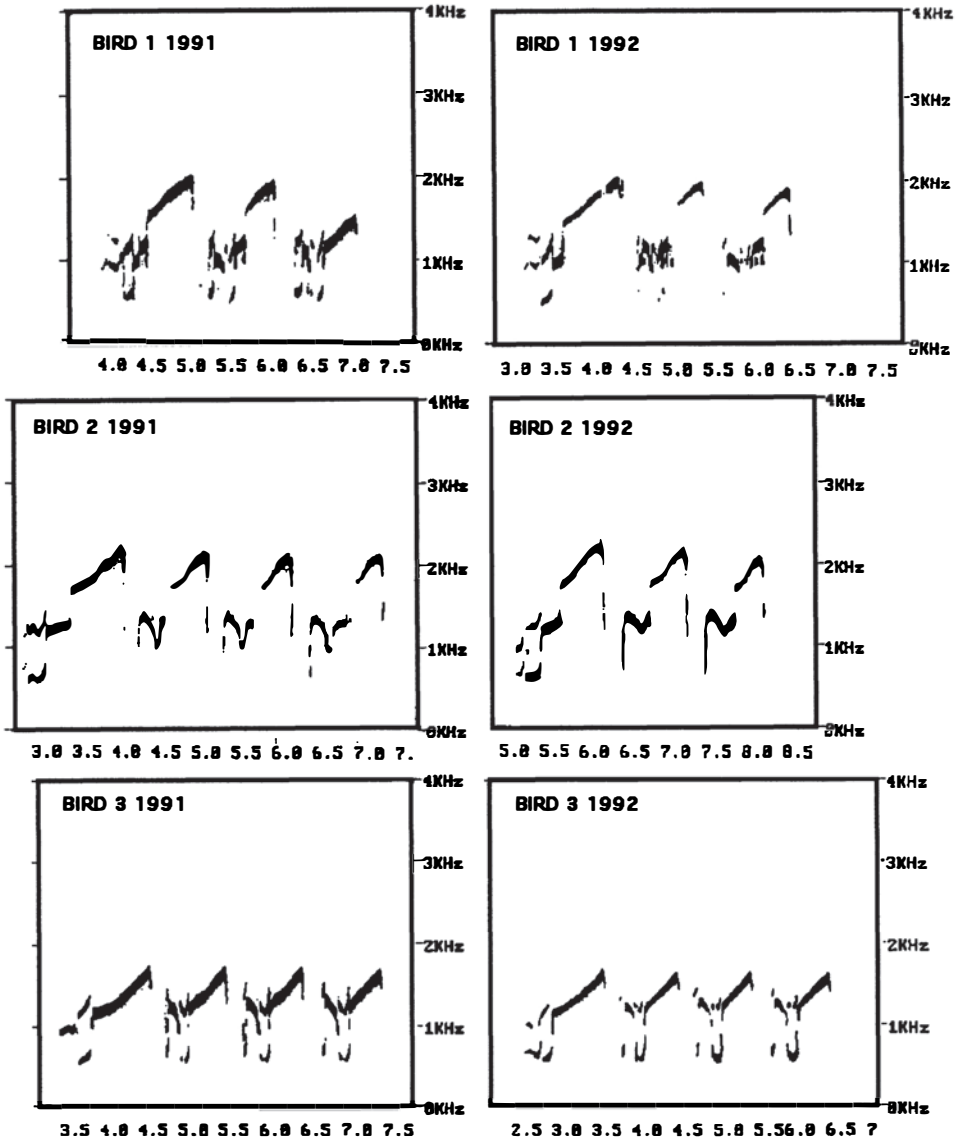

FIGURE 7. Spectrograms (time in secs., frequency in kHz) of the yodel call of three black-throated divers recorded in 1991 and 1992. Note the striking differences between individuals and the consistency between years. From Gilbert and McGregor in press.

[Espectrogramas (tiempo en segundos, frecuencia en kHz) de la llamada "yodel" de tres colimbos (*Gavia arctica*) grabadas en 1991 y 1992. Nótese las sorprendentes diferencias entre individuos y la consistencia entre años.]

Conservation

The need to conserve internationally rare species that may be locally abundant and cause economic damage is a frequent source of conflict between conservation and agriculture. One such case is the Greenland barnacle goose *Branta leucopsis*. A very high proportion of the population of this internationally rare bird over-winters on Islay, western Scotland, greatly reducing grass yields from the island's pastures (Percival & Houston, 1992). Following protective measures, numbers on Islay have steadily increased resulting in serious conflict between conservation bodies and local farmers. Part of the resolution of this conflict has been the setting up of refuge areas on the island, but attracting birds into and ensuring that they remain within these areas is a continuing problem. This is partly because individuals birds are very faithful to particular parts of the island (Percival, 1991). A combination of model flocks in the refuges and scaring outside the refuges has been used, with limited success. As has been shown by Drent & Swierstra (1977) and Inglis & Issaacson (1984), the ratio of vigilant to foraging birds in relation to the size of model flocks crucially affects the attractiveness of the flock to passing birds; for example too many models in a vigilant posture in a relatively large flock deters birds form landing (fig. 6); such an effect is just what one would predict from the theories developed in behavioural ecology in relation to flock size, vigilance rates and predator protection.

Actually finding out the numbers of a rare species can be fraught with difficulties, since censusing and marking techniques can cause an unacceptable level of disturbance. One useful approach to solving this problem makes use of the fact that certain types of call, particularly those associated with mating and territorial displays and social contact, may contain important information on mate quality and individual identity and therefore be individually very distinctive. Thus, recording of the call may allow a useful census and monitoring of individual survival involving very little disturbance. In doing this kind of work, it is essential to ascertain what is the most appropriate call to use, how easy is it to record, how clearly and consistently different is the call between individuals both within and between years. This approach is being successfully developed for two rare bird species in the UK by Gilbert & McGregor (in press). One of these is the black-throated diver, *Gavia arctica*. This species nests on remote lochs in northern Scotland and, although visually relatively conspicuous, it is very sensitive to disturbance and

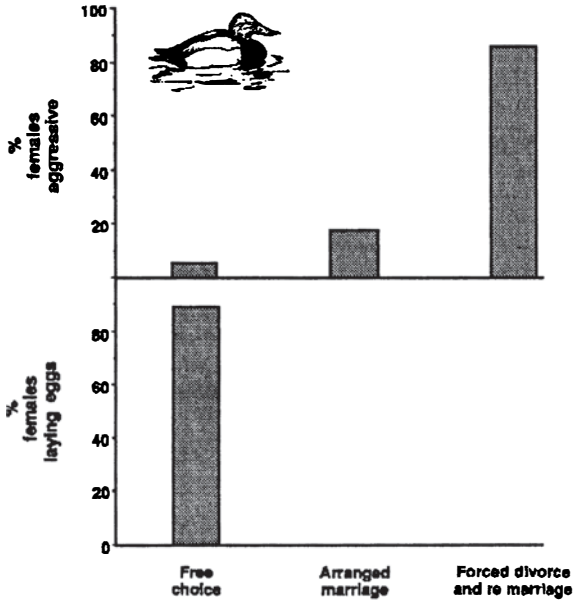

FIGURE 8. The level of female aggressiveness (upper graph) and proportion of females laying eggs in relation to the pair status in canvas backed ducks. Forced matings make females more aggressive and they do not lay eggs. From Bluhm 1985.

[Nivel de agresividad de hembras (gráfico superior) y proporción de hembras que ponen huevos en relación al estatus de la pareja en *Aythya valisineria*. Las apareamientos forzados hacen a las hembras mas agresivas y no ponen huevos.]

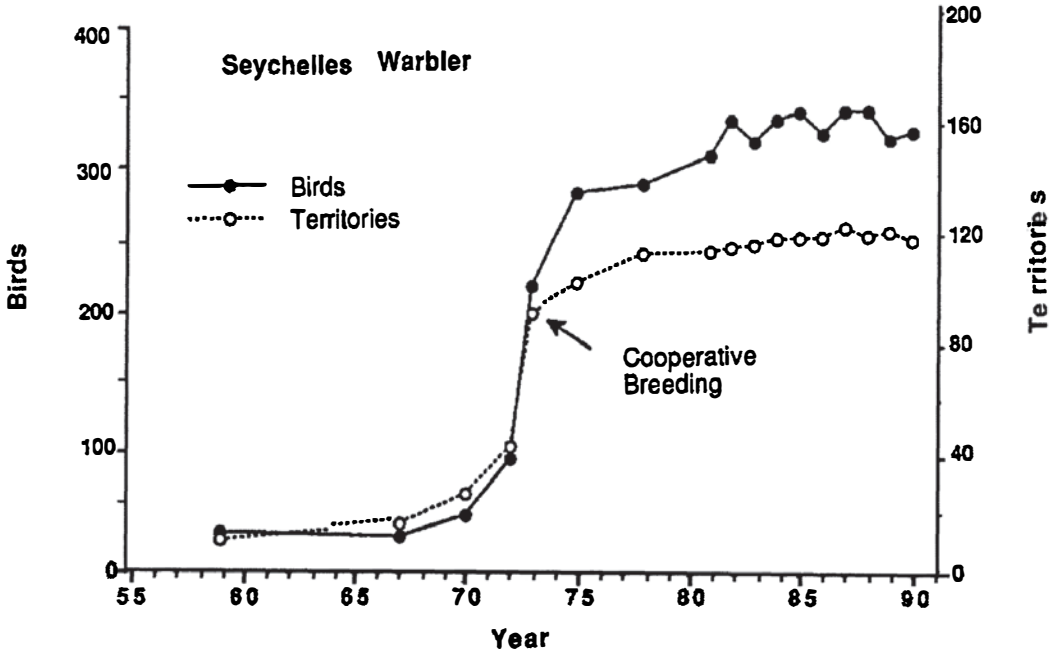

FIGURE 9. Changes in the number of Seychelles warbler breeding on Cousin island since the late 1950's. As the population stabilised, and the island became saturated with territories, co-operative breeding developed. From Komdeur 1992.

[Cambios en el número de *Acrocephalus seychellenis* nidificando en la isla de Cousin desde finales de la década de los 50. Cuando la población se estabilizó, y la isla se saturo de territorios, se desarrolló la nidificación cooperativa.]

difficult to identify individually. Gilbert & McGregor (in press) have shown that the 'yodel' call, commonly given when adults arrive at the breeding grounds and when they have young, is both easy to record and appears to be consistently different between individuals (fig. 7); recording this call thus offers an opportunity to obtain important information on numbers, survival and breeding fidelity. Furthermore, habitat management for rare species often takes little account of the need to provide, or simulate, the appropriate social environment, since the presence of conspecifics may be an important cue in habitat assessment (Reed & Dobson, 1993). Broadcast calls may, for some species, be a useful habitat management tool.

Captive breeding programmes are often used to replenish or maintain populations of endangered species in the wild. A large branch of behavioural ecology is concerned with the development of theory and collection of empirical data on the adaptive significance of mate choice. The need to allow animals to choose mates, even in captivity is emphasised by the consequences of not so doing. In canvas-backed ducks (*Aythya valisineria*) for example, forced pairing results in females being very aggressive and failing to produce eggs (fig. 8); some females actually kill the males they are forcibly paired with (Bluhm, 1985). In programmes

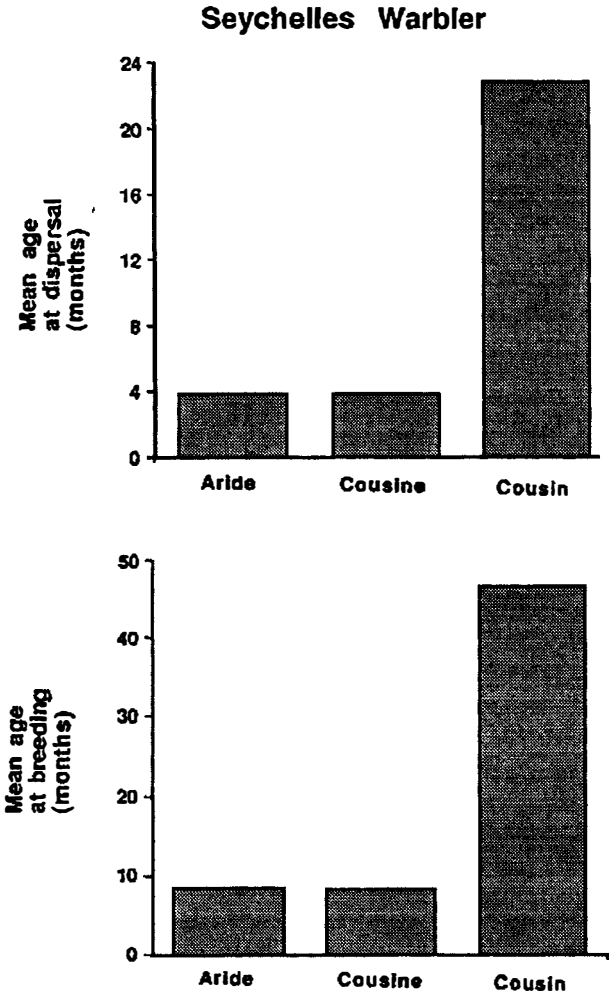

FIGURE 10. Changes in the mean age of dispersal from the natal territory (upper graph) and the age of first breeding (lower graph) in the Seychelles warbler when birds were introduced from the saturated Cousin island to the unoccupied islands of Cousine and Aride. From Komdeur 1992.

[Cambios en la edad media de dispersión del territorio natal (gráfico superior) y edad de la primera nidificación (gráfico inferior) en *Acrocephalus seychellenis* cuando se introdujeron desde la saturada isla de Cousin a las islas desocupadas de Cousine y Aride.]

like that for the almost extinct Californian condor (*Gymnogyps californianus*, getting captive birds to breed is crucial to the species survival. For this and other such programmes, it is essential to know how quickly adults remate if taken into captivity, will birds reared together form pairs, will birds show mate choice if housed in groups and do unpaired birds interfere with the mating of others? Answers to such questions are also pertinent to testing hypotheses concerned with the adaptive significance of mate choice. Recent data (Cox et al., 1993) suggest that in Californian condors mate choice is an important consideration in the success of captive breeding and that competition and interference also occur.

Working with rare species can provide the opportunity to carry out an experimental test of a theory that would not be possible with a common species, while at the same time conducting

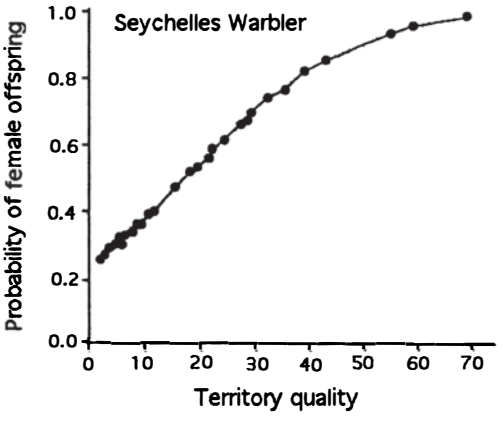

FIGURE 11. Offspring sex-ratio in relation to territory quality (measured by food-abundance) in the Seychelles warbler. Birds breeding in low quality territories produce more males. From Komdeur 1991.

[Proporción de sexos de la descendencia en relación a la calidad del territorio (medida en abundancia de alimento) en *Acrocephalus seychellenis*. Las aves que nidifican en territorios de baja calidad producen mas machos.]

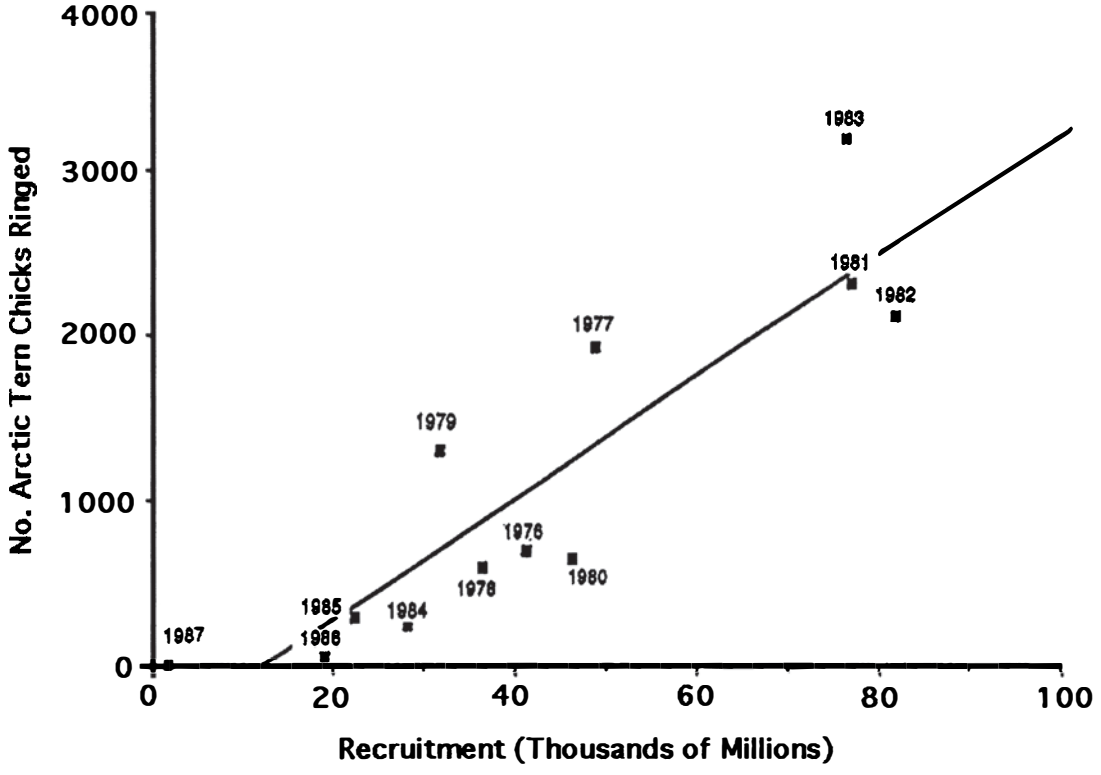

FIGURE 12. The relationship between young production and the production of young sandeels for Arctic terns in Shetland. From Monaghan *et* al., 1989.
[Relación entre la producción de jóvenes de *Ammodytes marinus* y *Sterna paradisaea* en Shetland.]

important conservation work. For example, the population of the Seychelles warbler (*Acrocephalus seychellenis*) fell to very low numbers in the early 1960's and the bird was confined to a single island in the Seychelles, Cousin island. However, successful management allowed numbers to increase and interestingly, as the habitat became saturated, co-operative breeding developed (fig. 9). To extend the species range, birds were transferred to two unoccupied islands, Aride and Cousine, which also provided an experimental test of the hypothesis that habitat saturation gives rise to co-operative breeding (Komdeur, 1992). Initially, co-operative breeding did not occur on the new islands, and both the age of dispersal and age of first breeding were considerably lower than on Cousin island, showing that habitat saturation played an important role in the development of co-operative breeding (fig. 10). Further, the data showed that the birds that helped established pairs were mainly females, but that only pairs on high quality territories benefited from having helpers. Komdeur (1991) therefore predicted that birds on poor quality territories should produce mainly male offspring, to reduce the probability

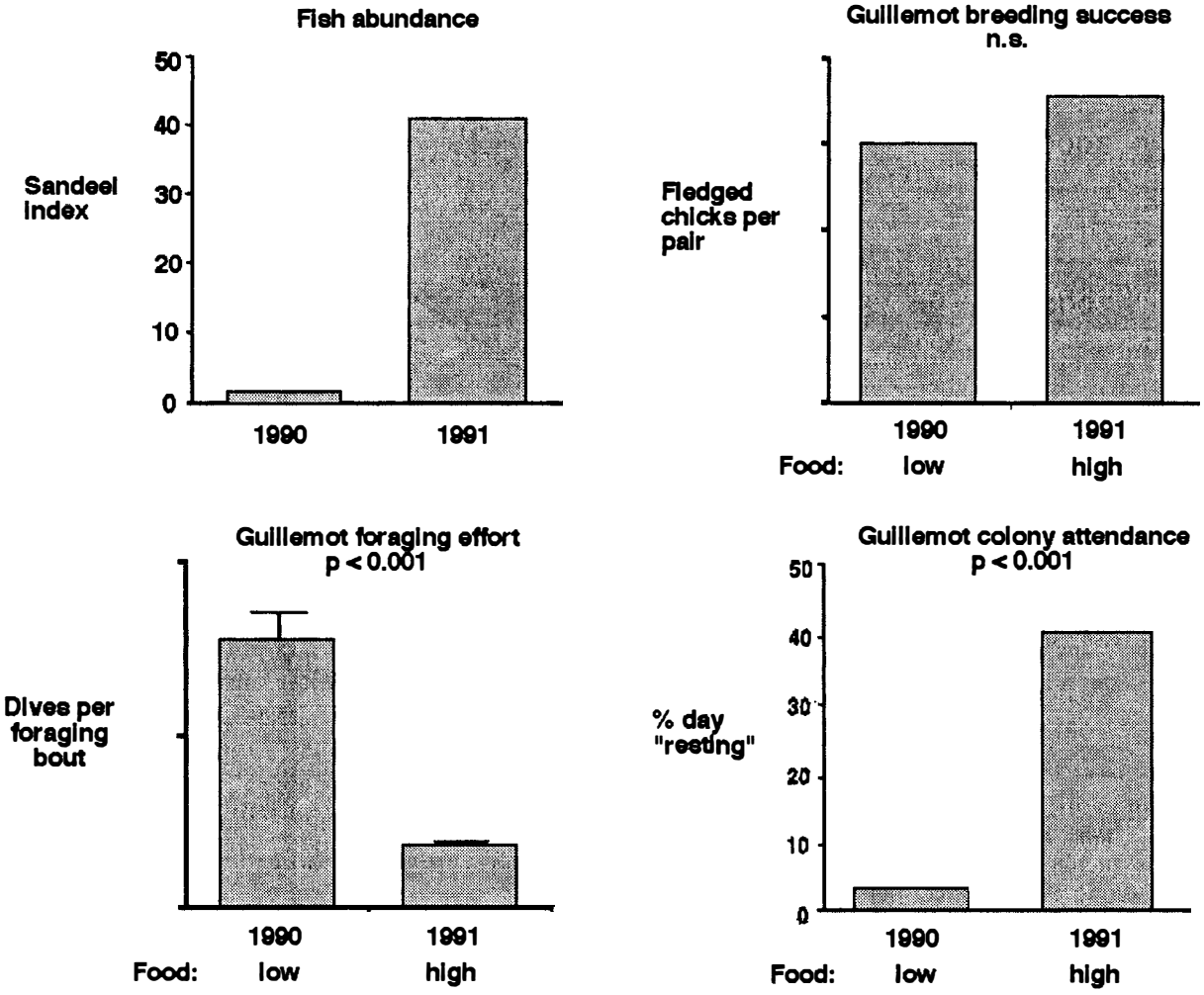

FIGURE 13. The effect of large changes in food abundance (shown in the tip left) on breeding success (top right), number of dives per bout of foraging (bottom left) and proportion of time spent at the colony by non-brooding birds (bottom right) for guillemots in Shetland. Only the behavioural parameters were affected. From Monaghan *et al.* and Uttley *et al.* in press.

[Efecto de cambios grandes en la abundancia de alimento (gráfico superior izquierdo) sobre el éxito reproductor (arriba a la derecha), el número de zambullidas por episodio de alimentación (abajo a la izquierda) y proporción de tiempo a en la colonia por aves no reproductoras (abajo a la derecha) para *Uria aalge* en Shetland.]

of having helpers, which he found to be the case (fig. 11). Such data, in addition to their conservation interest are of considerable interest to behavioural ecologists in general.

Understanding how the behaviour of some species relates to changes in the environment may provide useful information about environmental change *per se*. This is particularly useful in habitats where it is difficult to monitor change directly, as is the case with much of the marine environment. The need to take ecological effects into account in the management of marine fisheries has recently been recognised, but monitoring changes in fish stocks is both difficult and very expensive. The behaviour of marine birds can provide very useful information on fish stocks, but it is essential that we know which species to monitor and which parameters are sensitive to changes in food abundance. In species such as the Arctic tern *Sterna paradisaea*, breeding success itself can provide a useful indicator of changes in fish populations (fig. 12; Monaghan et al., 1989), but other species may continue to breed successfully despite large fluctuations in prey populations. This is illustrated by recent changes in sandeel *Ammodytes marinus* populations in the Shetland Islands, northern Scotland. A collapse of local sandeel stocks and the impact on breeding seabirds such as the surface feeding Arctic terns led to considerable conflict between conservationists and the fishing industry. The fact that some diving species such as the guillemot *Uria aalge* continued to breed successfully led to claims that the fish were still present but, having moved deeper in the water column, were no longer available to surface-feeding seabirds (Monaghan, 1992). However, detailed studies of guillemots both at the colony, and at sea using radio telemetry, showed that diving birds had altered the effort devoted to foraging, thereby mitigating the effect of reduced food supply on breeding success (Uttley et al., in press; Monaghan et al., in press); a comparison between two years of radically different food abundance (assessed by independent assessment of sandeel populations in the vicinity of the colonies) showed that, while there was no significant difference in breeding success between the two years, guillemots made more than 4 times as many dives per foraging bout and non-breeding birds spent much less time at the colony when the food supply was poor (fig. 13). Thus, in addition to providing information on the flexibility of foraging strategies and their effect on breeding success, this work has also shown that in guillemots behavioural parameters, such as time at the colony, provide more useful information on changes in fish stocks than do more ecological parameters such as the level of young production. In addition to providing information on changes in fish stocks, such work can also provide useful information on other changes in the marine environment. For example, following the wreck of the oil tanker, the 'Braer', off Shetland in January 1993, we have been able to assess sub-lethal effects of oil contamination of seabirds by examining detailed aspects of their foraging and colony-based behaviour.

Conclusion

All of the examples above represent studies that could have been carried out under the aegis of pure research. That they have been done on rare, pest or useful indicator species means that they have been of considerable practical significance and illustrates the usefulness of behavioural research in a wide variety of contexts. They also illustrate that an appropriate choice of species, when investigating a particular theoretical issue may provide additional and welcome practical benefits.

Resumen

Estudio del comportamiento animal: ¿cual es su

utilidad?

No es siempre fácil reconocer el valor práctico de los estudios de comportamiento animal, especialmente los que tratan de su significado funcional. Usando varios ejemplos, este trabajo revisa el valor práctico de los estudios de comportamiento animal, en particular con respecto a la mejora de la productividad de poblaciones manejadas, el control de plagas y problemas de conservación.

Acknowledgements

I would like to thank Gillian Gilbert and Tim Clutton-Brock for access to data in press and Neil Metcalfe for comments on an earlier draft of the manuscript.

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(Recibido: septiembre 1993)