Does natural selection brought about by infectious diseases influence the process of speciation in seabirds and other birds?

This note presents a hypothesis which cannot be tested as yet, because the necessary data are not available. However, the author hopes that this publication will add impetus to research on seabirds and marine Pinnipeds, as well as to other fields, such as the study of bird song.

Diseases cause appreciable mortality among most vertebrates. The infectious diseases of seabirds and marine pinnipeds, by analogy to Man, might be transmitted by contact with a carrier, arthropod vectors, sexual intercourse, droplet infection, direct physical contact or by contaminated food and water. The risk of transmission of an infectious disease is undoubtedly greatest at the breeding colony, where large numbers of these animals are brought into close proximity. Natural selection ought to favour those animals which minimise the risk of contracting a disease which might be fatal to them or to their offspring.

If a seabird (or a seal) returns to its natal colony to breed year after year, the spectrum of pathogens it will risk encountering will remain roughly the same. Should it visit a neighbouring colony, the spectrum of pathogens there is likely to be different. In human communities, most dangerous diseases survive in the population at endemic levels, and epidemics are relatively uncommon. Even when an epidemic occurs, the disease does not affect all the members of the population, but only a small fraction of the population. Naturally, exceptions occur. The Black Death (an epidemic of bubonic plague which swept Europe during the 14th century) killed almost a third of the population. Generally, however, a disease survives in the population indefinitely, affecting only a handful of individuals at one time. The reason for this is believed to be as follows. People are exposed to a wide variety of pathogens. Some of the antigens possessed by rare dangerous pathogens are also possessed by relatively harmless common ones. Infection with the harmless pathogens thus conveys a low level of immunity to attack by dangerous pathogens. Should the patient then be exposed to an infection with a small number of pathogens of the dangerous type, the infection is likely to be brought under control quickly.

Such infections are called sub-clinical infections in man, and the immunity conveyed is almost as effective as vaccination against the disease. It seems likely (though as yet unproved) that sub-clinical infections are responsible for conveying immunity to a large fraction of the population, where a disease is endemic, and the disease can only infect new individuals on rare occasions. Thus the disease remains rare. It should be clear that this mechanism for widespread immunity in the community requires that the harmless pathogens should also be present. Should they be absent from a population into which the dangerous pathogen is introduced, a serious epidemic could result. This might explain why smallpox was so lethal when first introduced into Fiji by European travellers. It became less dangerous as time went by, much too quickly for genetic resistance to be a possible explanation. Limited exposure to antigens from relatively harmless pathogens is believed to be the cause of the increased susceptibility to disease of young men from well-to-do families while undergoing military training, another fact which serves to underline the importance of sub-clinical infections in conferring immunity (British Medical Association 1989).

If these principles are also applicable to other animals which suffer from infectious diseases, it is possible to argue that the prevalence of infectious diseases could influence speciation.

Suppose that a species of seabird or seal breeds on two islands which lie some distance from one another (such as Great Shearwaters *Puffinus gravis* on Tristan/Gough and the Falklands). Suppose also that the spectrum of diseases on the two island groups is different. On Tristan/Gough diseases A, B, C, and D are present while on the Falklands diseases W, X, Y, and Z are present. Suppose that diseases A and Z are lethal to adults with high probability but normally exist at low endemic levels in the population because of widespread immunity. In order to be immune to A, a bird must first contract B, C, and D, after which it must contract sub-clinical infection with pathogen A. Conversely, in order to be immune to Z, a bird must first contract W, X and Y, after which it must contract a sub-clinical infection with pathogen Z. Naturally, Tristan/Gough birds will usually be immune to A but not to Z, while Falklands birds will usually be immune to Z but not to A. A Falklands bird which visits Tristan has never been exposed to A, B, C and D, and is just as likely to contract disease A as it is to contract any other disease. Until it contracts B, C, and D in sequence it will be highly susceptible to infection with pathogen A, and may well die of this disease if it contracts it. Similar arguments apply to Tristan birds which visit the Falklands. Generalising from this argument, a seabird which visits a colony other than the natal colony might run a serious risk of mortality due to infectious diseases, if the spectrum of diseases in the colony being visited is different from that at the natal colony. Thus, it ought to pay individuals to breed at their natal colony and not at any other.

There is another reason why it pays to breed at the same colony year after year. There are a number of diseases of man which cause discomfort in adults but little else, yet can be lethal to babies. Gastroenteritis and summer diarrhoea are excellent examples. If seabirds possess similar diseases which are potentially lethal to nestlings but not to adults, fidelity to the breeding grounds is expected. This is because an adult bird will have acquired most of the common diseases of the colony early during its life and would be unlikely to contract these same diseases again while nesting and transmit them to its chicks. Note that this protection does not extend to the chicks of adult birds which change their breeding colony frequently.

Natural selection ought to favour those individuals which breed at the same colony where they were raised. It is at their natal colony that they are likely to have the greatest fitness for the two reasons outlined above. Thus, fidelity to the natal colony is clearly predicted by the arguments presented here.

There is plenty of evidence for fidelity to the breeding site in seabirds. A case with which the author is familiar is quoted as an example. In the Maltese islands, the Storm Petrel *Hydrobates pelagicus* breeds only on the tiny islet of Filfla, and all Storm Petrels ringed locally are ringed on ringing trips to the Filfla colony. By 1988, a total of 14,194 Storm Petrels had been ringed on Filfla (Sultana & Gauci 1988). No Storm Petrel ringed on Filfla has ever been found breeding elsewhere in the Mediterranean (J. Sultana pers. comm. 1991).

By reducing gene flow between neighbouring populations, breeding site fidelity should accelerate speciation by helping to provide the reproductive isolation required for allopatric speciation. Fidelity to the breeding site goes a long way towards explaining how such wide ranging birds as seabirds could have speciated in allopatry.

Consideration of the interests of members of the colony leads to recognition of an additional factor. As an immigrant to a colony might be carrying a disease which does not occur in the colony, the immigrant is a potential threat to members of the colony. It pays members of the colony to signal to the immigrant that it is in a strange and potentially hazardous environment, while it pays the immigrant to recognise such signals and leave the colony. The mechanism by which such a scheme might operate might be as follows. Suppose that the seabirds of a population rapidly acquire social signals which convey the message that the bird belongs to a particular population. The signal might be a *learnt* variant of a call or display. Immigrants ought to be under strong selection pressure to recognise that the signal is alien, the implication being that it is in an unfamiliar colony and at serious risk of contracting a dangerous disease. It would be idle to suppose that the birds actually reason all this out. In all probability, they would evolve to feel ill at ease when surrounded by alien signals. This discomfort in the presence of alien signals is referred to here as Xenophobia. This Xenophobia should be based on the recognition by the immigrants of strangeness in the local dialect of a social signal.

Thus, if the spectrum of diseases found at various colonies of a species varies appreciably, two effects are predicted. (i) Local dialects of social signals ought to arise (ii) Individuals of a species ought to experience Xenophobia when they perceive strange signals.

Perhaps speciation by seabirds and pinnipeds is accelerated by Xenophobia. Immigrants to a colony might feel discomfort when confronted with strange animals and move off. This ought to reduce gene flow between populations and help to provide the reproductive isolation required for allopatric speciation.

The hypothesis presented here is clearly applicable to bird and mammal species which habitually breed in colonies. In addition, if a bird or a mammal species lives in two contiguous habitats across which the spectrum of pathogens differs appreciably, one would expect dialects of social signals to evolve. This should facilitate reproductive isolation and speciation if the contrast between the two habitats is sufficiently marked. It should be possible to devise a model for parapatric speciation using data from natural populations when sufficient data become available. For the moment, it should suffice to point out that many bird song dialects are associated with differences in habitat (Catchpole 1979) and even when they are not, the distribution of infectious diseases might be patchy enough to have given rise to the observed mosaic of song dialects. Some studies (quoted in Catchpole 1979) have shown that song dialects may represent one difference between populations which also differ from one another at an appreciable number of genetic loci. It remains unclear whether these song dialects arose because the populations were isolated sufficiently to differ genetically, or whether the song dialects helped to bring about the reproductive isolation which eventually led to the genetic differences, as hypothesised here.

The hypothesis presented here is incomplete in two important respects. No mention has been made of any possible mechanism by which dialects of social signals originate and become established. In addition, no reason has been advanced to explain how Xenophobia might be brought under control and speciation prevented. The hypothesis advanced here creates the impression that every isolated population should diverge to full species status, given sufficient time. This might well be untrue.

Some aspects of the hypothesis presented here are easiest to test using data collected at seabird colonies. Seabird colonies also permit a more convenient mathematical treatment of the problem, as the birds are confined to well defined geographical locations.

Finally, it should be stated that any animal intelligent enough to learn a variant of a signal and recognise strangeness in variants of that signal should show the phenomenon of fidelity to the breeding site and

Xenophobia, provided that it is sufficiently mobile for the choice to be meaningful. The phenomena are most easily observed in birds but might also be found in other animals.

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Male Spanish Sparrow *Passer hispaniolensis* run over by a car while fighting

Fights among Spanish Sparrows are common in February in Malta. The fighting birds flutter close together and push, grasp or scratch at one another with their feet. The fighting birds inevitably lose height, and sometimes fall to the ground, still locked in combat.

On 14 Feb1989, I was seated in a moving car on my way to work when two sparrows locked in combat appeared ahead of the car in a side road at Msida, a built-up area. They floated down to the ground just ahead of the car, and looking back through the rear window, I could see that one of the sparrows had been run over and lay crushed on the road surface. Later in the day, I returned to the scene of the incident on foot, and I could ascertain that the crushed bird was a male Spanish Sparrow.

This observation shows just how absorbed the birds were as they fought. The near approach of a bright red car passed unnoticed long enough for one of the fighting birds to be crushed by the wheels.

Clearly, models of fighting behaviour which ignore the risk of predation on the combatants by an alert predator, are simplistic when applied to fighting among prey species.

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Interspecific territorial behaviour among three species of *Turdidae* wintering in Malta

This note reports the results of several years of casual observations, and two winters in which observations were carried out more carefully. The behaviour of wintering Robins *Erithacus rubecula*, Stonechats *Saxicola torquata*, and Black Redstarts *Phoenicurus ochruros* has been observed in Malta for several years.

Their niches are largely separate because these species occupy different habitats. The habitats they occupy while they winter in Malta are listed in Table 1. The Maltese countryside is very varied topographically and severely disturbed by agriculture and urban development. As a result, many areas occur which *prima facie* might seem suitable for more than one of these species.