

# Convergent and divergent character displacement

P. R. GRANT\*

*Department of Zoology, South Parks Road, Oxford*

*Accepted for publication February 1972*

Consideration of the possibilities and difficulties of detecting character displacement leads to a re-definition of the phenomenon; character displacement is the process by which a morphological character state of a species changes under Natural Selection arising from the presence, in the same environment, of one or more species similar to it ecologically and/or reproductively. This incorporates the principal ideas in the original definition given by Brown & Wilson (1956), but eliminates the restriction of making comparisons of the character states of a species in sympatry and allopatry.

The evidence for the ecological (competitive) aspect of character displacement is assessed by analyzing in detail the best documented and well publicized examples in the literature. Some of the examples either do not exhibit displaced characters or, if they do, the "displacement" can be interpreted in other and perhaps simpler ways; this applies to the so-called classical case of character displacement, *Sitta tephronota* and *S. neumayer* in Iran. Other examples, involving lizards and birds, constitute better evidence for character displacement, but in no single study is it entirely satisfactory. It is concluded that the evidence for the ecological aspect of character displacement is weak.

## CONTENTS

Introduction . . . . .	39
Terms . . . . .	40
The types of character displacement . . . . .	41
The detection of character displacement . . . . .	42
A new definition of character displacement . . . . .	44
The evidence . . . . .	45
Individual examples . . . . .	
Mainland . . . . .	45
Islands . . . . .	51
Sets of examples: Islands . . . . .	58
Another type of convergence: Communication systems . . . . .	61
Conclusions and discussion . . . . .	63
Acknowledgements . . . . .	65
References . . . . .	65

## INTRODUCTION

Brown & Wilson (1956) drew attention to a known but neglected phenomenon of evolutionary importance revealed by systematic studies. They called it character displacement (Wilson & Brown, 1955) and defined it as "the situation in which, when two species of animals overlap geographically, the

\* Present address: Biology Department, McGill University, Montreal, P.Q., Canada.

differences between them are accentuated in the zone of sympatry [overlap] and weakened or lost entirely in the parts of their ranges outside this zone [i.e. in allopatry]", (p. 63). Several examples of the phenomenon were given, from a variety of taxa. The authors interpreted them as being the result of natural selection. Specifically, in sympatry selection was supposed to minimize (a) attempts at hybridization between the two species arising from mistaken identity, and (b) competition between the two species. These may be distinguished as (a) reproductive, and (b) ecological aspects of character displacement. In this article I shall be concerned solely with the ecological aspects of character displacement.

Numerous authors have purported to find evidence of character displacement in other groups of animals, mainly birds (Bock, 1970; Ficken, Ficken & Morse, 1968; Hutchinson, 1959; Nørrevang, 1959; Parkes, 1965; Ripley, 1959) but also lizards (Schoener, 1969a, 1970), mammals and corixids (Hutchinson, 1959), hominids (Schaffer, 1968) and cladocera (Deevey & Deevey, 1971). It has been widely accepted, to the point of being treated as an axiom in theoretical studies and with enlightening consequences (e.g. MacArthur & Levins, 1964). It has also contributed to a shift in emphasis away from the Gaussian principle of competitive exclusion (Hardin, 1960) and towards the question of how similar species can be without one competitively eliminating the other (e.g. Grant, 1966a; Lack, 1971; MacArthur & Levins, 1967; Schoener, 1965).

Largely as a result of these theoretical investigations, the opposite phenomenon, involving convergence in sympatry of characters with an ecological function, was considered, and deduced to be at least a theoretical possibility (MacArthur & Levins, 1967; MacArthur & Wilson, 1967; Schoener, 1969a). Subsequently evidence has been forthcoming (Grant, 1969a; Schoener, 1970).

How good is the evidence for both character displacement and sympatric convergence? The principal weakness is that the sole criterion used in their recognition is the difference between the character states of a species in sympatry and allopatry. Yet divergence or convergence in sympatry must certainly occur on some occasions for reasons not connected directly with the presence of another similar species. There is a clear need for a critical appraisal of the evidence for the ecological aspects of character displacement and convergence, and this paper attempts to provide it. It will first be necessary to examine the meaning of character displacement and how it can be detected. In the light of these considerations character displacement will be re-defined, and then the evidence for it assessed.

#### TERMS

##### *Character*

The features involved in character displacement and convergence may be morphological, ecological, behavioural or physiological (Brown & Wilson, 1956). In fact most of the evidence for character displacement is morphological. I shall restrict the term character to morphological attributes of animals, and consider parallel ecological, behavioural or physiological

phenomena as analogues. Thus displacement of an ecological feature, such as affinity to certain habitats, is an ecological analogue of character displacement. It may occur without any displacement of a morphological character.

It happens that in all the examples surveyed in this paper the morphological characters are part of the feeding apparatus of the animals. Since feeding is an ecological and not a reproductive function, it follows that a displacement of structures concerned with feeding have ecological consequences. If the feeding structures have, in addition, a species recognition function, as experiments indicate with some birds (Lack, 1947) then displacement may have reproductive consequences as well. The application of character displacement theory has been criticized for a failure to make this distinction clear (Birch, 1960). But in all the examples to be considered, except the geospizid example, species recognition is probably achieved in other ways because the two species of a sympatric pair differ conspicuously in other morphological and/or behavioural attributes.

### *Displacement*

Character displacement denotes a change of a character from one state to another by some force. Brown & Wilson (1956) make it clear that the force is natural selection arising from the presence, in the same environment, of another and similar species. Displacement in this sense is practically synonymous with divergence. Convergence is in the opposite direction to character displacement as the term is used by Brown & Wilson (1956). However, since the mechanism is the same in both cases, natural selection arising from the presence of another similar species, it seems logical to use the term displacement for both, but to contrast the direction and result of the displacement by the terms convergent and divergent. Thus character displacement, as used previously, will henceforward be replaced by divergent character displacement, and its opposite will be referred to as convergent character displacement.

Mayr (1963) suggested that the term divergence was preferable to the term displacement as used by Brown & Wilson (1956), because divergence was used by Darwin (1859) to refer to the same phenomenon (see reply by Brown, 1964). But divergence and displacement are complementary and both should be retained.

### THE TYPES OF CHARACTER DISPLACEMENT

Eight possible categories were recognized in an earlier paper (Grant, 1969a) on the basis of the direction and extent of character displacement. These are shown diagrammatically in Fig. 1, together with four more (numbers 9 to 12). For the sake of clarity the two species are assumed to have isomorphic, initially partly overlapping, normal distributions of the character in question. Displacement direction and extent is shown by the arrows.

Either one (7 to 10) or both species (remainder) undergo displacement, and these may be referred to as unilateral and bilateral respectively. The two may be displaced in different (1 and 2) or the same (3 to 6, 11 and 12) directions; in other words, there is two-way or mutual displacement, and one-way displacement. Finally, displacement may result in convergence (1, 3, 5, 7 and

9), divergence (2, 4, 6, 8 and 10) or neither (11 and 12). The last of these needs to be emphasized because hitherto it has not been appreciated that displacement, in the sense in which I use the term, can conceivably occur without a convergent or divergent result.

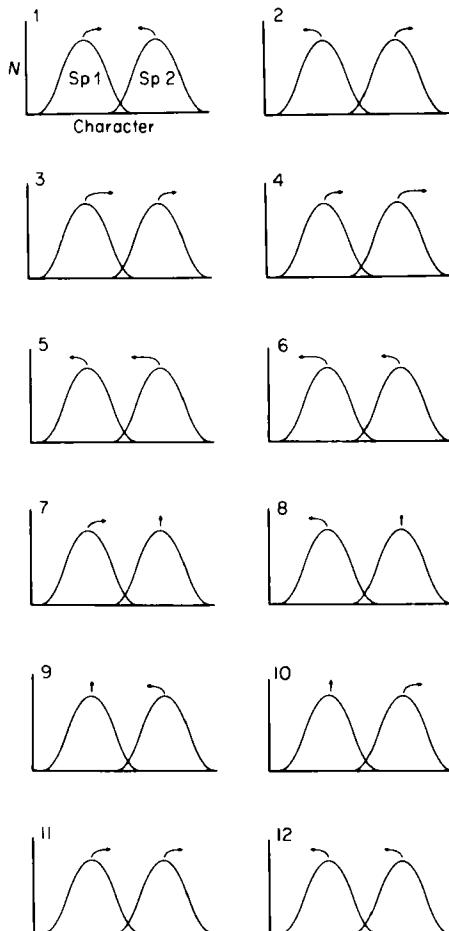


Figure 1. Twelve categories of character displacement based upon the direction and extent of change in a character state. Species 1 and 2 have normal distributions of a morphological character. When the two species meet they undergo a change in character state, indicated by the arrows, as a result of natural selection. A change in means is preceded by skewness in the distributions. Vertical arrows indicate no change. The possibility of the character states of the species "crossing over" is small (an example in Schoener, 1970) and is therefore omitted. Except for 11 and 12, which exhibit no net change in the difference between the species after selection, odd numbered models yield convergence and even numbered ones yield divergence.

#### THE DETECTION OF CHARACTER DISPLACEMENT

Changes of character state in a species, as a consequence of the geographical range of the species overlapping that of another, have never been observed and documented; they are inferred to have occurred from present-day, more or less static, distribution patterns (Fig. 2). The character state in allopatry is assumed to be the same as that at the time of initial contact between the species. The

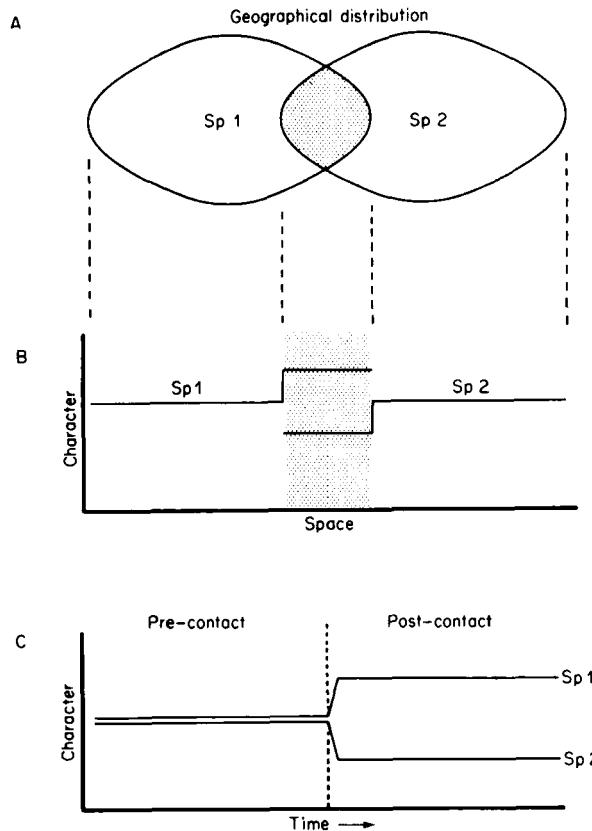


Figure 2. Character displacement inferred from character states in sympatry and allopatry.

state in sympatry is therefore the post-contact state, and the state in allopatry is the pre-contact state. A simple comparison of the two present-day states of a species yields a difference which is attributed to the influence of the other species. Paraphrasing Brown & Wilson (1956), the populations in the allopatric zones serve as “controls” for the observations in the sympatric zone.

Aside from the fact that present-day populations may not be the same as they were when, in part of their ranges, the crucial events are supposed to have occurred, there are two main difficulties with this procedure. The movement of animal distribution may have been from sympatry to allopatry rather than the assumed reverse. Secondly the species might not be the same in the sympatric and allopatric zones for reasons independent of the presence of another similar species; in fact all of the patterns of character change illustrated in Fig. 1 could be generated in ways in which interspecific (competitive) influences play no part.

Brown & Wilson (1956) were aware of the first difficulty: “Of course in this case (Slave-making *Formica* ants), as in all others under present consideration, there is no way of determining how much “displacement” has occurred as a process in the sympatric populations as opposed to “convergence” in the unispecific one. The final pattern observed may in fact be the result of one of

these two processes alone", (p. 58). This difficulty can only be resolved by making a judgement, often on the basis of highly indirect evidence, on the question of whether or not there was movement from an allopatric zone, such as the one observed today, to the sympatric zone. It is immaterial whether present allopatric or sympatric zones correspond exactly in position with past ones or not (they may not, due to climatic changes, etc.).

Where allopatric zones are large it is reasonable to assume that allopatry preceded sympatry on the grounds that the species were formed in allopatry (Mayr, 1963), particularly if the systematic relationship of the species is so close that they were probably derived directly and fairly recently from a common ancestor. But where the allopatric zone of one or both species is small, peripheral and isolated, such as an island, it is more logical to consider the present allopatric zone to have been established by animals moving from the sympatric zone. In such cases the character state in allopatry cannot be considered as a "control" for events in sympathy, since it is a derived and not original condition. Brown & Wilson (1956) refer to similarity in allopatry as "convergence". This is correct in those instances where the allopatric state is derived from the sympatric state. It is not convergent character displacement however, since no displacement has occurred, but it is convergent character "release", i.e. a character "released" from the constraints imposed by the presence of another species. Note that the term release can be applied to mean or variance (amplitude; Wilson, 1961) aspects of a morphological character or an analogue; here I am solely concerned with the mean.

The second difficulty is in establishing that the character state of one species in sympathy is really influenced by the other species. It is not sufficient to show that allopatric and sympatric character states of a species are different, because if such a difference is found it might be attributable to influences other than a coexisting species. These other possible influences must be considered. An approach to this problem can be made by describing the variation, if any, of the character state in allopatry, and then asking what influences the character state and its variation in allopatry? Given the answers, and on the basis of this information only, a prediction can then be made as to what is expected in the zone of sympathy if the other species has no influence. Essentially, this constitutes a null hypothesis which stands to be accepted or rejected by a comparison with the observed character state in the zone of sympathy.

In summary, the detection of character displacement involves making judgements on two questions; (a) what was the pre-contact character state, and (b) is the difference between pre- and post-contact character states attributable to selection arising from the presence of the other species, or to some other cause?

#### A NEW DEFINITION OF CHARACTER DISPLACEMENT

The foregoing considerations make it desirable to re-define character displacement, as follows. Character displacement is the process by which a morphological character state of a species changes under natural selection arising from the presence, in the same environment, of one or more species similar to it ecologically and/or reproductively. The antithesis is character release, which can be defined in the same way except that the word absence is

substituted for the word presence. Character displacement and character release can be brought together under the general term character shift.

The advantages of this definition of character displacement over Brown & Wilson's are (1) it is defined as a process and not as a result, which means that alternative results can be recognized as being the product of essentially the same process; thus (2) it is not specifically tied to a comparison of sympatric and allopatric character states (instead character states can be compared in two areas of sympathy, or at two times in sympathy with the aid of fossils); further, (3) it incorporates convergence, and also the possibility of no change in the difference between the species after displacement. (4) It makes explicit the fact that change is directly attributable to the presence of another species. (5) It is not restricted to two species, nor even to animals; the recent recognition that the reproductive aspect of character displacement occurs in plants (Levin, 1970) makes this a necessary feature of a definition. (6) It does not include character release because this is a different phenomenon.

Detection of examples of character displacement is not made easier by excluding character release from the above definition of character displacement. But the inclusion of character release, as was done implicitly by Brown & Wilson (1956), makes the definition, and hence the use of the term, less precise.

The least satisfactory feature of the new definition is the vagueness of the adjective similar applied to the species. Systematically related might be preferred but, like similar, it gives no indication of how much.

#### THE EVIDENCE

Although character displacement has been invoked many times to account for differences between sympatric species, in several cases it has been no more than just mentioned as a possibility. The following survey treats only the examples most prominent in the literature, those in which an attempt has been made to demonstrate that character displacement has occurred. Most of the examples involve birds, probably because birds have received the most attention from those interested in interspecific competition due largely to the influence of Lack (1944, 1947) and MacArthur (1958).

#### *Individual examples*

##### *Mainland*

(1) *The Rock nuthatches* (*Sitta neumayer* and *Sitta tephronota*) are partly allopatric and partly sympatric in south-eastern Europe and Asia. In sympathy (Iran) they are markedly different in bill size (and facial patterns), whereas in allopatry they are intermediate and almost identical. Since food size is related to bill size (Baldwin, 1953; Betts, 1955; Morris, 1955; more recent studies Hespenheide, 1966; Kear, 1962), Brown & Wilson (1956) see this as an example of two species, originally allopatric, becoming sympatric as their ranges changed, and in sympathy subject to selection for divergent, and hence different, feeding characteristics (category 2, Fig. 1). Thus "divergent" selection for different feeding ecologies and morphologies, akin to disruptive

selection on a single species, has minimized interspecific competition for food, and this has resulted in stable coexistence over an appreciable area.

The above interpretation makes sense if geographical variation in bill size within each of the sympatric and allopatric zones is ignored. But it is evident from the original data given by Vaurie (1950, 1951), and subsequently reproduced by Mayr (1963), that bill length varies with longitude within each of the zones. Therefore a sounder procedure is to ask what is to be expected of a species in the sympatric zone if the other species has no influence, given the pattern of variation in the allopatric zone.

This procedure can be adopted with *S. tephronota* by using regression analysis. There are enough data for this species given by Vaurie (1950) to make it possible to calculate regression lines in both allopatry and sympatry, and then to compare them. If there is no character shift in sympatry attributable to the presence of the other species, the slopes and intercepts for the sympatric and allopatric regression lines should be the same. If the other species has had an influence, this should manifest itself as a different intercept on the  $y$  axis, due to a "step" in the cline (Fig. 3), and possibly as a difference in slope.

Because the sexes differ in mean bill length, and because the sexes are unequally represented in the samples, only the data for males (the best represented sex) have been used. Mean bill length for each of the localities given by Vaurie has been regressed on longitude. The results are shown in Fig. 4 and Table 1. In allopatry there is a highly significant correlation ( $r = 0.97$ ,  $P < 0.005$ ); in sympatry there is a strong correlation ( $r = 0.82$ ), but this is not

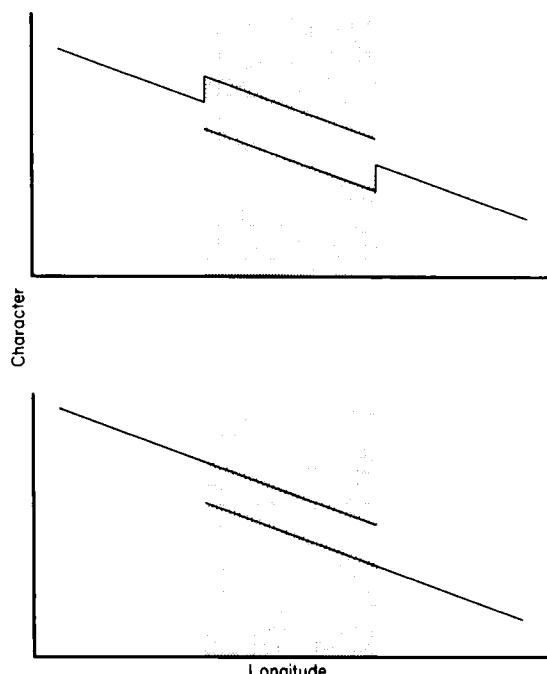


Figure 3. Geographical variation in character states of two species which do (1) or do not (2) exhibit character displacement in sympatry (stippled). The sharpness of the step in thecline, (1), is exaggerated for illustrative purposes; in fact a less "angular" step is to be anticipated as a consequence of gene flow across the sympatry/allopatry border.

significant, largely because of inadequate sample size. The slopes and the intercepts of the two calculated regression lines are almost identical (Table 1). As shown in Fig. 4 an extension of the allopatric regression line into the zone of sympatry fits the bill length data in the sympatric zone as well as does a line calculated on the basis of the sympatric points above. Therefore bill length variation in allopatry "predicts" bill length variation in sympatry, and there is no need to resort to explanations of character displacement for this species.

Table 1. Regression parameters for bill length of *Sitta tephronota* and *S. neumayer* on longitude

Species	Region	Slope ( $\pm S\bar{x}$ )	Intercept
<i>S. tephronota</i>	Allopatry	-0.154 $\pm$ 0.019	36.67
<i>S. tephronota</i>	Sympatry	-0.159 $\pm$ 0.078	36.89
<i>S. neumayer</i>	Sympatry	-0.153 $\pm$ 0.042	30.76

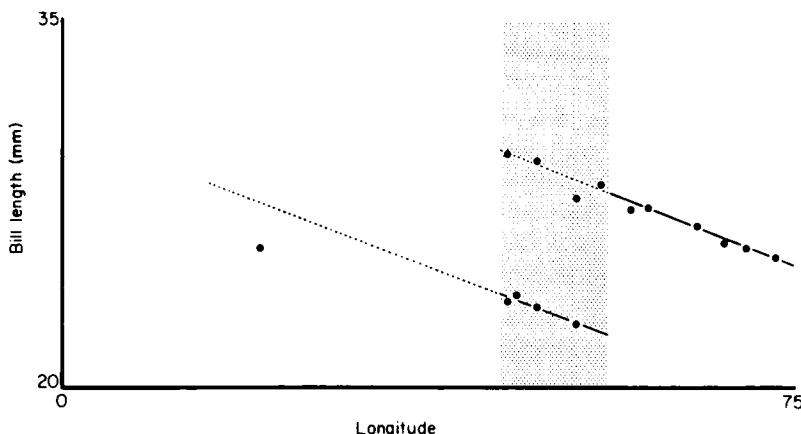


Figure 4. Geographical variation in mean bill length of *Sitta tephronota* (upper) and *S. neumayer* (lower). The broken lines are projections of calculated (solid) regression lines fitted by the least squares method. Stippling indicates sympatry.

This procedure cannot be followed with *S. neumayer*. Vaurie (1950) does not give the measurements of individual specimens, and there are only two allopatric localities listed, one of which is represented by only six specimens (sexes combined). So that a comparison can be made with the above result, Vaurie's four sympatric means have been read off his fig. 3 and regressed on longitude to see if the slope is similar to that of *S. tephronota*. The calculated correlation is once again high ( $r = 0.93$ ), but like the sympatric data of *S. tephronota* it is not significant ( $d.f. 2, P < 0.1 > 0.05$ ), probably for the same reason. Data from both sexes were used in this calculation, so the slope would not be expected to be identical to the slope for sympatric *S. tephronota*. Nevertheless the slope of the line is  $0.153 \pm 0.042$  (S.E.) which is almost identical with that of sympatric *S. tephronota* ( $0.159 \pm 0.078$ ). Thus in sympatry the two species vary geographically in like manner. Obviously the intercepts are different.

To see if sympatric variation of *S. neumayer* is different from allopatric variation the sympatric regression line can be extended into allopatry, and the one reliable data point compared with it. That single point refers to Greece and Dalmatia combined, which covers a large band of longitude (approx 15° to 26°). The regression line extended into the allopatric zone "predicts" a mean bill length in this band of longitude between 26.8 and 28.5 mm. The observed is only 25.8 mm.

The deviation of the observed from the predicted may be due to the unequal representation of the sexes in the sample of measurements. A firm conclusion cannot be drawn from such a result. But it does raise the possibility that the clines in sympathy and allopatry are different. If the slopes of the sympatric and allopatric regression lines are the same but their intercepts different, this means that a step in the cline at the sympathy-allopatry border brings *S. neumayer* closer to *S. tephronota* in sympathy than would be predicted from a knowledge of variation in allopatry alone, i.e. convergence (Fig. 5). If, on the

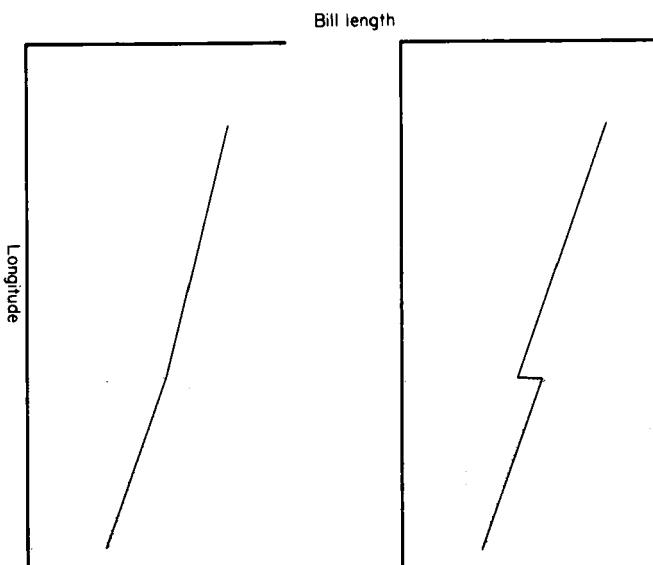


Figure 5. Alternative patterns of geographical variation in *Sitta neumayer*. Stippling indicates sympathy.

other hand, the slopes are different and change at the sympathy-allopatry border, then divergence occurs in sympathy because the slope must be steeper there than in allopatry. It is not obvious why either of these alternatives should occur. A study is planned to document geographical variation of this species in allopatry in more detail in order to resolve this difficulty.

Thus a comparison of character states in sympathy and allopatry, with attention paid to geographical variation, yields the conclusion that *S. tephronota* has not undergone divergent character displacement of bill length in sympathy with *S. neumayer*. *S. neumayer* has probably not undergone character displacement either, but the possibility cannot be ruled out that it has diverged. On the other hand the difference in bill length between the species in sympathy facilitates their co-existence. Correlated with differences in

the bill are differences in feeding; for example in Iran the larger *S. tephronota* is capable of breaking open almond nuts to extract the kernels whereas the smaller *S. neumayer* has not been observed to do this (L. Cornwallis, pers. comm.).

There is a possibility that geographical variation in bill length is no more than an allometric consequence of geographical variation in body size in relation to climate (i.e. Bergmann's and Allen's rules; see e.g. James, 1970). In the absence of a more direct measure, wing length can be used as an indicator of body size. Wing length of *S. tephronota* varies geographically in a similar manner to bill length, only with an ostensibly steeper slope. There is no indication of a substantial difference between the relationship of wing length and longitude in sympatry and allopatry respectively (Table 2). If body size and proportions vary geographically, chiefly in relation to climate as it affects thermoregulatory needs, then the limits to the sympatric zone (cf. Lack, 1971) may be set by the maximum and minimum size within which the Rock Nuthatch body plan can operate efficiently. The smallest birds (*S. neumayer*) of either species are found at the eastern limit of the sympatric zone, and the largest birds (*S. tephronota*) of either species at the western limit.

Table 2. Regression parameters for wing length of *Sitta tephronota* on longitude

Region	Slope ( $\pm S\bar{x}$ )	Intercept
Allopatry	$-0.290 \pm 0.147$	106.62
Sympatry	$-0.395 \pm 0.224$	114.58

(2) *The Tree nuthatches.* Ripley (1959) interpreted patterns of geographical variation in bill size in other members of the genus *Sitta* in the light of Brown and Wilson's theory. He gave reasons for believing that character displacement (with divergence) had occurred in two situations in Asia, illustrating his point with diagrams of bill shape but with an unsubstantial set of measurements. It does not seem worth examining this in detail because Lack (1971) has outlined reasons for believing that the two pairs of species do not coexist in the same environment; members of one pair (*S. nagaensis* and *S. yunnanensis*) occur in different habitats, while members of the other pair (*S. nagaensis* and *S. himalayensis*) are separated by habitat and altitude. But, even if more detailed field studies were to show that the species did coexist in the same habitat, or that they encountered each other in contiguous habitats, it is by no means clear that character displacement need be invoked to account for geographical variation in bill size. For example, bill size increases in an easterly direction (contrary to the Rock nuthatches) in both *S. nagaensis* and *S. himalayensis*, and perhaps body size does too. The area of sympatry is at the western part of the range of the smallest species, *S. nagaensis*, where it is small, and near the eastern limit of the range of the larger *S. himalayensis* where it is particularly large. As with the Rock nuthatches, the difference between sympatric and allopatric character states of a species may be entirely due to clinal variation in body size and parts.

(3) *North American warblers.* The most detailed example of possible character displacement has been given by Ficken *et. al.* (1968). They have supplied ecological as well as morphological information on two warbler species, *Dendroica pinus* and *D. dominica*. The two species occur sympatrically in southeastern States including Delaware, Maryland and Virginia (Delmarva) and allopatrically in southern Florida and northeastern States (*D. pinus*) and the midwestern States (*D. dominica*). Bill length distributions of the allopatric populations are almost identical, whereas the bill length distributions of the sympatric populations are completely non-overlapping. These facts are interpreted as evidence of character displacement.

There are no significant differences between sympatric and allopatric populations of *D. pinus*, and no indication of clinal geographical variation. Therefore this is a possible example of one-way, divergent character displacement, category 12, with *D. dominica* diverging from *D. pinus* in sympatry. On the other hand *D. dominica* does display clinal variation, increasing in bill length from south to north. There does not appear to be a sharp discontinuity in the cline, except in Florida. In addition there is variation in relation to habitat; birds in coastal pine and mixed forests tend to have larger bills than those in inland deciduous forests. This may account for the apparent discontinuity in Florida. Several times *D. dominica* were observed feeding from the cones of loblolly pines in Delmarva. Their long bill evidently enables them to reach between the bracts to the stalk of the large cones.

These two types of eco-geographical variation would appear to dictate that the *D. dominica* with the largest bills are those living in northern coastal areas with pine forests, i.e. at Delmarva. It is not necessary to invoke character displacement to account for the large bills of the Delmarva birds. Moreover, from the ecological information given there is no reason to believe that *D. dominica* has changed its use of habitats or feeding patterns in response to the presence of *D. pinus*, even though individuals of the latter are generally dominant to *D. dominica*. If character displacement has occurred it has been obscured by the other patterns of geographical variation.

Ficken *et al.* (1968) were aware of this difficulty. They tried to circumvent it by comparing the bill lengths of birds (*D. dominica*) collected in pine and non-pine forests from a locality in North Carolina. The absence of any indication of difference between these samples led them to reject the idea that variation in relation to habitat accounted for the large bills of Delmarva birds. However, their attempt to eliminate a complicating habitat influence is unsatisfactory. Their analysis presupposes that birds in non-pine forest are adapted specifically to that forest and not to nearby pine forest or both, and this may not be correct. Moreover their samples were only four birds from pine and two samples of six birds from non-pine forest so a difference, if it exists, would have to be conspicuous to be detected. The difficulty remains that the large bills of the Delmarva birds can be accounted for without recourse to character displacement. Despite being the most detailed case of supposed character displacement, more information is needed.

(4) *North American mammals.* Suggestive evidence of character displacement in carnivores and granivorous herbivores has been presented by McNab (1971). Geographical variation in body size (head-body length) was found to conform to the following pattern in species of the carnivore genera *Mustela* (4 spp.),

*Martes* (2 spp.) and *Felix* (2 spp.); clinal size change occurs in the absence of a congener of similar body size, but in the presence of a similar congener there is no size change with latitude or longitude. Most of these particular clinal size changes are in accordance with Bergmann's rule. The lack of expression of Bergmann's rule in the geographical area of overlap is attributed by McNab to (divergent) character displacement.

A different indication of displacement is given by squirrels. In the Pacific states the only large tree squirrel, *S. griseus*, has a body size intermediate between the sizes of the two eastern squirrels, *S. carolinensis* and *S. niger*. We have already met the phenomenon of allopatric intermediacy, interpreted as evidence for character displacement, when considering the Rock nuthatches (*Sitta*).

McNab's purpose was to show that Bergmann's rule is poorly supported by North American mammals and to offer, as possible explanation, the over-riding influence of character displacement. The evidence for character displacement is therefore no more than suggestive. It is difficult to accept for more than that because the data are inadequate and not controlled for age-dependent variation. In the graphs relating body size to latitude or longitude the lines drawn among the points are biased towards showing a change in body size corresponding with the boundary of geographical overlap (presumably sympatry) and non-overlap (allopatry). And there are large differences between some of the congeneric species (*Martes* spp., *Felix* spp. and possibly some *Mustela* spp.) in diet and habitat in both sympatry and allopatry, which raises doubts as to whether differences in body size between sympatry and allopatry are functionally related to interspecific competition. Perhaps, in some instances, geographical variation (or the absence of it) in predator size is related to geographical variation (or the absence of it) in prey size alone, irrespective of whether a congener is present or not. McNab suggested this for *Blarina*. More detailed study is required to substantiate the character displacement hypothesis applied to mammals in North America, and to examine its applicability on other continents, especially as Rosenzweig (1968) has concluded that neither interspecific competition or size of available prey are likely to be responsible for geographical variation in predator size.

### *Individual examples*

#### *Islands*

(1) *Darwin's finches*. The oft quoted example of character displacement involves *Geospiza fuliginosa* and *G. fortis* on the Galapagos Islands (Brown & Wilson, 1956; Lack, 1947). They are sympatric on many islands, and allopatric\* on the small islands Daphne (*G. fortis*) and Crossman (*G. fuliginosa*). Where sympatric they differ markedly in bill length, where allopatric they have intermediate and nearly identical bill lengths. It is likely that the small island, allopatric populations were derived from the large island, sympatric populations, rather than *vice versa* (Lack, 1947). Therefore this is an

\* There is some doubt that they really are allopatric. Lack (1945) refers to three specimens of *G. fuliginosa* collected on Daphne, and more recently M. P. Harris (pers. comm.) has observed both species sympatric on this island. Crossman has not been reported on since 1906; possibly both species occur there too, although the small size of the island leads one to expect only one of them.

example of character release, but not of character displacement. Even this may not be correct (Bowman, 1961; Amadon, 1966).

From which populations originally allopatric (Lack, 1947) were the sympatric populations derived? The answer is not known. Movements between islands have been frequent enough for the two species to have spread throughout the archipelago, making it impossible to identify the starting populations. This being so it is not possible to detect character displacement in sympatry, even if it has occurred. Assuming that the two species had their origin in allopatry, either they diverged in allopatry, adapting to local and different conditions, and were already markedly different when they first met, or else they were similar when they first met and selection produced divergent character displacement.

(2) *Birds on the Cape Verde Islands.* Brown & Wilson (1956) presented reasons for believing that character displacement had occurred three times on these islands. The data were taken from a paper by Bourne (1955a). In fact the data look more like evidence for character release and its ecological analogue.

The island warbler *Acrocephalus brevipennis* is derived from a mainland species of similar body size. It has an absolutely and proportionately larger bill than its mainland relative, as do many other birds in island situations (Grant, 1965; Murphy, 1938). An increase in bill length was considered by Wilson & Brown (1956) to be the product of selection in an environment characterized by the absence of potentially competitive congeners. Therefore it is an example of character release.

Similarly a species of kite, *Milvus milvus*, occupies the habitat on Cape Verde which, on the mainland, is occupied by the related *M. migrans*. This should properly be considered an example of ecological (habitat) release.

The third example given by Brown & Wilson (1956) is less easy to analyse because it is not clear what is the original and what is the derived population. The seabirds *Calonectris (=Puffinus) diomedea* and *P. puffinus* are coextensive in parts of the Northern Hemisphere, but are found separately on the Cape Verde Islands (*C. diomedea*) and parts of Europe (*P. puffinus*). Their bill lengths are different in sympatry, but intermediate and nearly the same in allopatry. No precise data are given, so although character displacement in sympatry is a possibility, two alternatives cannot be ruled out: (1) clinal geographical variation can account for the observed differences between allopatric and sympatric bill lengths of each species, without recourse to interspecific influences; (2) allopatric populations are derived from sympatric populations and exhibit character release.

The first alternative is indicated by the information given by Palmer (1962). The northernmost subspecies of *C. diomedea* is the largest and the southernmost subspecies, on Cape Verde Islands, is the smallest. Similarly for *P. puffinus* birds breeding in higher latitudes tend to be larger than closely related forms breeding in lower altitudes; but there is an interesting exception. Disproportionately large birds occur in the western Mediterranean (*P.p. mauretanicus*). This is in the zone of sympatry. It appears to constitute an example of character convergence and not divergence, because *P. puffinus* is the smaller of the two species; even so the difference in bill length between the species is as much as 40% (calculated from data given by W. R. P. Bourne in Palmer, 1962).

Three facts indicate that an increase in bill size in sympatry is not directly associated with the presence of *C. diomedea*. First, there is a disproportionately large form of *P. puffinus* in the Pacific off Baja California (*P.p. opisthomelas*), a counterpart to *P.p. mauretanicus* and at approximately the same latitude. It is not sympatric with another Shearwater species. Second, both *P.p. mauretanicus* and *P.p. opisthomelas* are unusual in migrating northwards to cooler climates after an early breeding season. *P.p. mauretanicus* migrates to the Bay of Biscay, English Channel and North Sea, whereas *C. diomedea* migrates to the Atlantic, and moves south before returning to breed (Bourne, 1955b; Palmer, 1962). Third, bill size is approximately correlated with wing length in *P. puffinus*, as indicated by the data in Palmer (1962). Thus the disproportionately large size of *P.p. mauretanicus* can be interpreted as a result of selection upon a species which is seasonally subjected to lower temperatures than it would be if it stayed the year round at the latitude at which it bred, or migrated to lower latitudes. A general response (overall size) to climate rather than a specific response (bill length) to food is indicated, without any obvious adjustment of bill size to the presence of a potential competitor.

The morphological character undergoing displacement might be body size rather than bill size, because in seabirds food size is more strongly correlated with body size than with bill size (Ashmole, 1968; the same is true for flycatching birds, Hespenheide, 1971). Nevertheless, for the same reasons as given above, there is no obvious adjustment of the body size of *P. puffinus* to the presence of a potential competitor.

Later Bourne (1957, 1963) introduced a third and smaller species, *P. assimilis*, into the discussion of possible competitive effects. It is a better candidate for character displacement because the geographical variation in wing and bill length runs in the opposite direction to that of *P. puffinus*; it is smaller on the Azores, Madeira and Canary Islands, where it is sympatric with *P. puffinus* and *C. diomedea*, than on the Cape Verde Islands where it coexists with the much larger *C. diomedea* only. Furthermore, *P. assimilis* and *P. puffinus* were originally allopatric in the opinion of W. R. P. Bourne (pers. comm.), so divergent character (bill) displacement of *P. assimilis*, possibly of both species, on the north Atlantic Islands is indicated. These species are receiving further attention from Dr Bourne, and it is to be hoped that the possible competitive effects on morphological characters will be clarified.

(3) *Bird species sympatric on islands and mainland.* Character shifts in island populations are often examples of character release, because they have been occasioned by the absence of competitor species with which they are sympatric in mainland situations. But there are some instances in which congeneric species are sympatric on both island and mainland, and have undergone character shifts on the island (Grant, 1966a). Hitherto they have not been considered examples of character displacement because the definition of displacement has involved a comparison of character states in allopatry and sympatry. However they can be so considered under the present definition.

Two chickadee (tit) species of the genus *Parus* on Newfoundland, two woodpecker species of the genus *Centurus* on the Mexican island of Cozumel and two heterogeneric species of hummingbirds on the Mexican Tres Marias Islands differ in bill length by a greater amount than do their mainland counterparts (Grant, 1966a). The (derived) island populations have changed in

opposite directions. Is this mutually divergent character displacement (category 2)? The hummingbird situation is complicated by the fact that the islands are lacking other hummingbird species, smaller and larger than the two present, which are present on the mainland. So character displacement, minimizing competition for possibly a low variety of resources on the islands (Grant, 1966a, 1969a), is one possible explanation of the divergence, and character release permitted by the absence of other, trophically similar, species is another. Both may be applicable.

As far as is known this complication does not enter the interpretation of the character shifts of the *Centurus* and *Parus* species. Therefore these two species pairs may constitute examples of character displacement, and merit further investigation. Doubtless other unsuspected examples exist.

(4) *Double-invasion species pairs of birds.* These constitute another class of examples worth examining for evidence of character displacement. Because of the restricted nature of the definition of character displacement they have not been examined from this point of view before (but see Bock, 1970; Nørrevang, 1959).

Double-invasion species pairs are those pairs of species on islands which are thought to owe their origin to two colonizations from a single stock on another island or mainland. In the interval between colonizations the first colonists develop almost if not complete reproductive isolation from the parental stock, so that when the second colonists arrive the two behave as distinct species. The observation which leads to this interpretation of events is that two species on an island are more similar, and presumably more closely related, to a third species elsewhere than either is to a fourth species.

In such cases there is usually no doubt as to which are the derived populations and which is the original one, nor is there doubt as to the order of colonization since one species is much more similar to the "parental" species (it may be the same, and/or only subspecifically different) than is the other and is therefore presumed to have colonized most recently.

Differences in bill length between sympatric double-invasion colonists are known to be large (Grant, 1968, 1972a). Either the first colonist changes before the second one arrives, and neither undergo appreciable change after the second one arrives, or else character displacement occurs following the arrival of the second colonist. Hence large differences in character state between sympatric, double-invasion, species pairs are not in themselves evidence for character displacement. To distinguish between the two it is necessary to know the character states of the two species at the time of arrival of the second. Knowledge of the character state of the first colonist at this time is generally unobtainable, although there may be grounds for assuming that the first colonist has remained unchanged since the arrival of the second colonist. That is to say, as far as the first colonist is concerned, either it undergoes undetectable character displacement or does not change. What is most unlikely is that the first colonist remains unchanged until the second colonist arrives, and changes only then. The second colonist does not present the same problem, because its pre-contact character state can be assumed, under most circumstances, to be identical or nearly so to the present character state of the founding population on another island or mainland. Evidence for character displacement may be sought with the second colonist.

Regrettably, in most instances available details of the founding population are not sufficient to enable the necessary comparison to be made between it and the second colonist. This could and should be remedied. The double-invasions in the Hawaiian archipelago are treated separately (below). There remains one situation which can be analysed.

Norfolk Island has been colonized not twice but three times by *Zosterops lateralis*. The first colonists differentiated into a highly distinctive species, known as *Z. albicollis*. The second colonist also changed, and it too is recognized as a distinct species, *Z. tenuirostris*. The third colonization known to have occurred took place in 1904 (North, 1904), and this population has remained unchanged, or else has changed to a small extent only (Grant, 1972a). Character release in the first two colonists has not occurred, because the founding *Z. lateralis* is not sympatric with a congener on the mainland. Possibly character displacement has occurred. If it has, it is of the category 4 type, since both species increased in bill dimensions prior to the arrival of the third colonist (the categories in Fig. 1 cannot be applied strictly to this example because the sympatric species are derived from a single species, not two as illustrated in the figure). The direction and extent of change is inferred from a comparison of the first two colonists with the third. The third is assumed to be similar to the first two at their time of arrival. This may be incorrect, but there is no evidence for or against it.

The difficulty with accepting this as evidence for character displacement is that something about the island environment may select for large bill size, and has operated on the first two colonists in the same direction but to a different extent because they have been there for different lengths of time. Against this it may be argued that the bill shape of the two is quite different, and whereas *Z. albogularis* exceeds *Z. tenuirostris* in bill depth and width, the reverse is true for bill length (Grant, 1972b). Clearly the two have not followed identical evolutionary pathways, which might be expected if there was no interspecific interaction. The different pathway followed by the second colonist, *Z. tenuirostris*, is evidence for character displacement. Possibly *Z. albogularis* has undergone displacement as well.

(5) *Birds in the Hawaiian archipelago.* Bock (1970) has used data published by Amadon (1947, 1950) on the Hawaiian subfamily of Honeycreepers, Psittirostrinae, to construct a model of the evolutionary changes occurring in an adaptive radiation. His thesis is that major evolutionary changes and the origin of new taxa result from adaptive radiations that are generated by series of micro-evolutionary changes. In an archipelago, such as the Hawaiian islands, individual islands are colonized by the same stock (species) more than once. During the intervals between successive colonizations the original and derived populations develop reproductive but not ecological isolation, so that when a second colonization takes place interbreeding does not occur but competition does. The result is selection for different feeding ecologies and associated morphological characters (divergent character displacement) leading to stable sympatric coexistence. Earlier Brown (1958) had pointed out that multiple colonizations of an area might be followed by multiple character displacements, yielding greater degrees of specialization, and Nørrevang (1959) had specifically interpreted some of the double-invasion phenomena on the Hawaiian islands in terms of character displacement.

The procedure adopted by Bock (1970) was to use geographical, systematic and bill size information to establish which species or subspecies had given rise to which. This enabled him to construct a linear series of probable evolutionary changes, which could be interpreted as a series of character displacements. Bock stresses that the evolutionary sequences represent "pseudophylogenics" rather than actual phylogenics: but in the absence of actual phylogenics he must use the pseudophylogenics to infer patterns of invasion and displacement.

The resulting model is so complex that it is difficult to assess the validity of its units by applying the criteria outlined earlier. The difficulties can best be shown with an example.

*Loxops virens* is deduced to have colonized Kauai twice (Amadon, 1950) from the fact that two species of *Loxops* on that island are both more similar to a species (*L. virens*) on other islands than to any other in the genus. The first invasion of Kauai and subsequent evolutionary change there gave rise to a small-billed form, *L. parva* (Amadon, 1950). The second invasion gave rise to a reproductively isolated form, *L.v. stejnegeri*, which has a longer bill than *L. parva* and all other populations of *L. virens*. This is taken to be an example of divergent character displacement; either category 2 or 12 in Fig. 1, depending upon whether the difference in bill length between *L. parva* and other island populations of *L. virens* is statistically significant or not (at present this is not known). Thereafter "the presence of a [relatively] small curve-billed prober, *L.v. stejnegeri*, on Kauai resulted in displacement of bill size in the Kauai population of [*Hemignathus*] *lucidus* to the larger billed form *H.l. hanapepe* which in turn resulted in displacement of bill size in the Kauai population of *obscurus* to the larger billed species *H. procerus*" (Bock, 1970: 715). In other words each invading species was influenced by the resident closest in size, but did not influence the resident.

The difficulty in assessing these interpretations lies not in identifying original and derived populations but in identifying pre- and post-contact character states. The initial step in this sequence is character displacement of the two *Loxops* species on Kauai. The evidence for it is derived from a comparison of these two with the descendants of the presumed original stock, *L. virens*, on neighbouring Oahu. The comparison is valid, at least for the second colonist, if it can be assumed that *L. virens* has remained unchanged and uninfluenced by other species. But this is unlikely because there are, or were, other species on Oahu which could have influenced *L. virens*. There are two species in the same genus, *L. maculata* and *L. coccinea*, which were ultimately derived from *L. virens* somewhere in the archipelago. There are also two species of *Hemignathus*, *obscurus* and *lucidus*. Since, from the argument above, *L. virens* has influenced *H. lucidus* on Kauai, it might in turn have been influenced by it on Oahu. The assumption of no change in *L. virens* on Oahu while so much was supposed to have taken place on Kauai is not necessarily incorrect but does not appear to be strong. I take this to mean that the presence of derived populations (of other species) in the zone of allopatry complicates a comparison of allopatric (original) and sympatric (derived) populations. The same objection can be raised with the other examples of character displacement in the archipelago proposed by Bock.

Like the *Zosterops* example discussed earlier there are differences between the members of a double-invasion *Loxops* species pair in shape of bill as well as

length. These differences in shape can be attributed to character displacement for the reasons given earlier. However the likelihood of change in the original population between the two colonizations, and subsequently, raises the possibility that the founders of the two colonist populations were quite different, and that the differences in bill shape arose largely or entirely in allopatry.

A related problem is extinction, which has happened to some of the presumed ancestors of pairs of species supposed to have undergone character displacement. The absence of the original stock renders unquestionable identification of character displacement impossible. Most recent extinctions in the archipelago are probably due to direct and indirect human influence (Warner, 1968), but there is less certainty that this is so for the species encountered by the first visitors to the islands and never seen since (examples in Amadon, 1950). Whatever the reasons, some links in the evolutionary chains are either missing or imperfectly known. An outstanding example is to be seen on Maui. *Hemignathus lucidus* is considered to have given rise to *Pseudonestor xanthophrys*, which in turn gave rise to *Psittirostra psittacea* (Bock, 1970). Each member of the series is sympatric on Maui; *Pseudonestor* occurs nowhere else. Did the process of speciation, proceeding to differentiation at the generic level, take place on Maui in sympatry? Did it occur allopatrically on Maui? This is possible because the island is second only to Hawaii in size and maximum elevation. Or did it, as seems most likely (see Mayr, 1963), occur in geographical isolation on different islands, with subsequent sympatry on Maui developing from colonizations from previously isolated populations on other islands? If this third alternative is correct, the initially allopatric populations have gone extinct (*Pseudonestor*), or undergone evolutionary change on those other islands. The pre-contact character state of all three species cannot be seen today. The high probability that the ancestral stock has become extinct makes it difficult to assess the suggestion by Bock (1970) that character displacement has occurred several times in the genus *Psittirostra* on the island of Hawaii. Five species of the genus are known from the island and only one, *P. psittacea*, on the other islands. The uncertainty of the origin of the five species on Hawaii is reflected in the statement "It may be possible that some *Psittirostra* arose on Hawaii via geographic isolation on different mountains, or the entire series of species arose by repeated invasions" (Bock, 1970: 717). Moreover three of the four species endemic to Hawaii have become extinct.

Despite these difficulties of assessing the evidence, and hence drawing firm conclusions with regard to character displacement, there is one additional piece of evidence that Bock (1970) overlooked. The difference in mean bill length between males and females of a species in the genus *Loxops* is smaller on Kauai and Hawaii, where double invasions have occurred, than on the other islands where the original *L. virens* stock is represented by a single species (Table 3). The difference between the sexes is greatest on Oahu; the data given by Amadon (1950) and shown graphically by Bock (1970) show no overlap between male and female distributions of bill measurements. There is some indication that the same phenomenon is exhibited by *Psittirostra psittacea* (see Amadon, 1950, for measurements). Since there are strong grounds for believing that the Kauai and Hawaii populations of *L. virens* were derived from Oahu and Lanai populations respectively, the differences can be interpreted as evidence

Table 3. Intersexual convergent character displacement in mean bill length of some double-invasion species of birds on Hawaiian islands. Data from Amadon (1950), in which mean ( $\bar{x}$ ), sample size ( $N$ ) and range but not standard deviation or standard error are listed. The interpretation of the second example as a double-invasion is Bock's (1970)

Species	Population	Island	$\delta \bar{x}(N)$	$\varphi \bar{x}(N)$	% difference
(1) <i>Loxops virens chloris</i>	Original	Oahu	14.9 (16)	12.9 (9)	15.50
<i>L. parva</i>	Derived	Kauai	12.7 (13)	11.7 (8)	8.55
<i>L.v. stejnegeri</i>	Derived	Kauai	19.2 (7)	17.8 (9)	7.86
(2) <i>Loxops virens wilsoni</i>	Original	Lanai	14.9 (7)	13.5 (2)	10.37
<i>L. sagittirostris</i>	Derived	Hawaii	20.7 (5)	19.5 (6)	6.15
<i>L.v. virens</i>	Derived	Hawaii	13.9 (18)	12.7 (15)	9.45

for convergent character displacement between the sexes in the presence of a competitor species. When the competitor species is larger selection causes a greater change in the larger sex, and when the competitor is smaller selection produces a greater effect on the smaller sex. It should be noted that the opposite phenomenon, divergent character release between the sexes, is known from studies of woodpeckers (Selander, 1966; Selander & Giller, 1963). Island populations of certain woodpecker species are sympatric with fewer woodpecker species than are their mainland relatives from which they were derived. The island populations are often more strongly sexually dimorphic in bill dimensions than are the mainland ones. A sexual isolation function of the divergence is unlikely, but a reduction in intersexual competition for food is plausible and supported by ecological evidence (Selander, 1966). Similar character shifts, in opposite directions, are exhibited by the two sexes of some species of gulls (Smith, 1966). These are also probably related to intersexual competition for food although a reproductive function cannot be ruled out because males undergo character (bill size and shape) shifts more than females, and females may use bill shape as a visual cue in mate discrimination and selection.

#### *Sets of examples: Islands*

(1) *Anolis lizards in the Antilles*. Schoener (1970) studied the many species of *Anolis* lizards on Antillean islands, and found evidence in the aggregate of convergence and divergence in each of the highly positively correlated characters of head length and snout-vent length. Over a range of predator sizes head length is directly related to mean prey size (Schoener, 1968; Schoener & Gorman, 1968). In view of this, and for other reasons (Schoener, 1969a, b; 1970), Schoener favoured an ecological interpretation of these character shifts. It involved competitor species and the need to exploit food supplies efficiently.

The analysis was made with many sympatric and allopatric pairs of species. Generally, the largest one-third of males was measured in order to obtain an estimate of adult size unhindered by subadults. Comparison of allopatric and sympatric character states of a species yielded differences in almost every

instance, some trivial and some large. All were considered and a group result was obtained. By this approach the question can be asked, are species generally more, or less, similar to a congener when sympatric than when allopatric?

The answers were as follows: (1) If the perch characteristics ("structural habitat") of two species in allopatry are similar, then the character states in allopatry are similar too, but these character states are more dissimilar in sympatry than in allopatry. If it can be assumed that the sympatric condition was derived from the allopatric, and not vice versa, then the above result can be restated as divergent character displacement in sympatry occurs more frequently than convergence. (2) This is because the small species show a strong tendency to become smaller upon contact with a congener, as deduced in the manner above, whereas the larger species show an approximately equal tendency to become larger or smaller (as with some bird species: Grant, 1969a), depending on how large they are in allopatry. If, in allopatry, the larger of the pair is much larger than the other species, there is a strong tendency for it to converge towards the smaller species in sympatry; if larger by a small amount, divergence in sympatry is the rule.

The above results are statistically respectable, so they cannot be attributed solely to sampling errors. Differences in character states of a species in sympatry and allopatry, and between species in sympatry, undoubtedly exist. However, as unequivocal evidence for character displacement in sympatry, the data are unsatisfactory for several reasons. First, in the absence of knowledge about original and derived populations, one has no basis for choosing between character displacement and character release explanations (see also Williams, 1969). This a stricture common to all archipelago situations (e.g. Galápagos, and Hawaiian islands). Second, in most cases the range of one species was contained entirely within that of another, so only one of a pair occurred in an allopatric zone. As a consequence, character displacement can be detected in only one of them. Third, uncontrolled factors having nothing to do directly with the presence of a congener, such as predators, climate, etc., might account for the difference in character state between sympatric and allopatric populations of that one species in some instances. Reproductive isolation may also be involved in some of the examples. These factors might be responsible for the (statistically) significant differences between allopatric and sympatric character states, and sampling errors can account for the remaining non-significant differences. Schoener (1970) considers these other factors to be unimportant in general, but does not examine their possible importance in the particular cases where differences between sympatric and allopatric character states are large (and probably statistically significant). Lastly, only the direction of character shifts was considered and no account was taken of the degree of difference between sympatric species that resulted from character shifts. Inferences concerning divergence or convergence may be wrong therefore. For example, both species might undergo a reduction in head length following the establishment of sympatry, but whether this is divergence or convergence is dependent upon the resulting sizes. It might yield a net divergence (Fig. 1, category 6), convergence (category 5) or neither (category 8).

Thus these data tell us more about conditions of coexistence than how these conditions are brought about. Nevertheless, despite these reservations, character displacement in sympatry as a result of selection minimizing the

deleterious effects of interspecific competition for food is a plausible explanation of the difference between allopatric and sympatric character states. It is supported by one additional fact. Soulé (1966) showed with lizards of the genus *Uta* on islands in the Gulf of California, and Schoener (1969b) showed with *Anolis* lizards, that the body size of a species was inversely related to the number of sympatric congeneric species. A species was largest on islands where it was alone, and different species tend to be the same size and large where solitary (Schoener, 1967). This strongly suggests that as an island receives successive lizard species colonists, selection favours smaller body sizes among resident and invading species due to some interspecific effect.

Schoener (1969b), in the most comprehensive explanation offered to date, suggests that the effect is competition for food. He points out that *Anolis* species have several age-size classes which overlap spatially and which take, in combination, a wide range of food sizes. Therefore the addition of a competitor species will reduce the available food across the spectrum of sizes more or less uniformly. As a consequence selection favours a reduction in body size because energy requirements are less and because efficiency with the (abundant) small items is high; presumably the large food items are too rare for any one species to subsist on them. The net result is smaller differences in body and head size between species in a species-rich than in a species-poor community, due to convergent character displacement towards small size (category 5). If this is correct the same phenomenon is to be expected in other animals which have several age classes which overlap spatially, such as some mammals, fish and insects. In contrast birds do not have several age-size classes, and with them divergence is expected because a competitor reduces the available food selectively, and not uniformly. Hence the response of residents and invader, under selection, is to exploit those resources of different size which the competitor exploits least.

(2) *Bird species in the Antilles.* A similar approach was used earlier by Grant (1969a) with less extensive samples of birds from the same region. Derived (island) and original (mainland) populations were identified, and bill lengths compared to see what changes had occurred in the island environment. Trivial changes, i.e. character shifts of less than 5%, were ignored, leaving five examples of convergence and five examples of divergence. All five divergences were one way with bill length increased (category 4), all but one of the convergences were mutual (category 1). Thus among these species the essential difference is the direction taken by the larger species. Examination of the data reveals that it is the species distinctly larger than a congener on the mainland which have converged towards a congener on the island. Schoener (1970) found a similar pattern among the *Anolis* lizards.

The difficulty of accepting these character changes in the island environment as clear evidence of character displacement is that they may be the products of character release instead. Most, if not all, of the species involved are sympatric with more congeners on the mainland than on the islands, and with more potential competitors in other genera too. Furthermore the examples of divergence may be the product of selection for large body size, with allometric consequences to bill size, that has nothing to do with competition. Character displacement may be the correct explanation for some of the character changes, but a more detailed study is needed to establish it.

*Another type of convergence: Communication systems*

Plumage and voice are reproductive characters of bird species, and should not be considered here except that they could undergo character displacement with ecological consequences (in relation to competition) under some circumstances.

Orians & Wilson (1964) drew attention to the fact that interspecific territoriality can be an alternative to divergent character displacement if one or more of the following conditions are met. The species (a) occupy simple habitats, (b) have stratified feeding habits, and (c) exploit the same food resource. Interspecific territoriality is facilitated by a similarity of the communication systems of the species. In territorial establishment and defence the systems are visual (plumage and posture) and auditory (song). Cody (1969) has suggested that species undergo *convergent* shifts in plumage and voice characters under the influence of selection for efficient interspecific communication. This happens, he argues, where habitat characteristics are intermediate between the optima for the two species, allowing no separation of the species into different habitats. The ecological consequence of convergent character displacement is a spatial separation of the species. Once effected, there is no further competition for food until the territorial system breaks down, if it does, at the end of the breeding season. In principle the displacement process should be experienced by other animals, such as mammals, which use olfaction in communication, but this is unknown in practice because such animals have not been studied from this point of view.

Many examples are given in support of this interesting suggestion, including salamander species (*Plethodon* and *Desmognathus*), but not one of them constitutes convincing evidence of convergence to facilitate spatial separation of the activities of the species. As Cody observes, a detailed knowledge of most of the species is lacking; this applies to both morphological and ecological characteristics. Most importantly the difference between sympatric and allopatric character states is not known in most cases.

In some instances interspecific territoriality does not seem even to be likely, and the similarity in plumage is probably attributable to other causes. For example, pairs of African Bush Shrike species of the genus *Malacorhynchus* are strikingly similar to each other in plumage features in sympatry, but the bill of the "*Malacorhynchus*" member of each species pair is half as long again as the bill of the "*Chlorophoneus*" member (differences in weight are even greater; see Hall *et al.*, 1966). Such a difference in bill length strongly indicates a difference in diet (see also Jackson, 1938). It is similarity, not difference, in diet which is a usual correlate of interspecific territoriality (Grant, 1966b; Orians & Wilson, 1964). Furthermore, strictly speaking the plumage characteristics of each species pair show parallelism (Hall *et al.*, 1966) rather than convergence. Hall *et al.* (1966) discuss the possible causes of the parallelism in terms of mimicry and in terms of a common response to the same environmental conditions by systematically related species. Cody (1969) offers the suggestion of convergence as an alternative for those examples, including this one in his view, where "similarities in appearance or voice . . . seem much more exact than can be accounted for by common ancestry or response to similar ecological gradients" (p. 237). The choice, on this basis, of examples for consideration must pose formidable problems.

In other instances, even though the species are known to hold territories interspecifically, there is no evidence for convergence, but rather an indication of a lack of divergence. For example, two species of wrens of the genus *Thryothorus* are sympatric over a large part of Mexico, have nearly identical bill lengths and diets, defend territories against each other and communicate with nearly identical songs (Grant, 1966b). Cody (1969) refers to this as an indisputable case of vocal convergence. In fact there is no evidence that they have converged from a previously more different state. There are no tape-recordings of the songs in allopatry, but I have heard a few allopatric birds on the Mexican mainland (Sinaloa, Oaxaca) and was not impressed that they were different from sympatric birds. I suggested that selection had favoured similarity of song in sympatry as a means of effecting spacing out of potential competitors for environmental resources (Grant, 1966b). This is another way of saying that selection acts against divergent individuals of either species. It does not necessarily imply convergence. If the two species already had similar songs in allopatry when they first met convergence would not be possible. Thus selection maintaining pre-existing similarities is, I believe, a simpler explanation of how the present situation arose than one involving convergence. Cody (1969) makes the same point about lack of divergence, but with another pair of interspecifically territorial species, the North American titmice *Parus inornatus* and *P. wollweberi* (also Cody, 1970).

The other example of convergence in song involves North American Meadowlark species, *Sturnella magna* and *S. neglecta*. Unlike the *Thryothorus* wrens it is known that their songs are more similar in sympatry than in allopatry (Lanyon, 1957). But similarity of song here is probably due to a combination of reasons; to hybridization, even though at a low frequency now, and to the fact that an individual of one species can add to its inherited song a component learned from a neighbouring individual of the other species. Convergent evolution of the two species has not necessarily occurred, other than through hybridization.

The case for convergence in sympatry, in examples where there is no difference between sympatric and allopatric character states of a species, can only be upheld by assuming that the convergent character spreads from sympatry to allopatry and throughout the species range. According to Cody this can happen by dispersal of individuals possessing the "converged" character into the allopatric zone, and breeding with allopatric individuals. Cody stresses that this will happen if there are no attendant disadvantages in allopatry, but does not consider the selective advantage the individuals possessing the trait must have in allopatry if their genotypes are to be differentially propagated there. Where there are no differences between sympatric and allopatric character states it is surely simpler to assume that similarity is due to common ancestry. The most detailed example of supposed convergence in plumage or song to effect spacing out (Cody & Brown, 1970) is also subject to criticism on similar grounds (see also L.L.S. 1971, *Auk*, 88: 211), as is the supposed convergence exhibited by sunbirds (*Nectarinia* spp.) in Africa (Cheke, 1971).

Convergent character displacement of song and plumage in sympatry remains to be demonstrated. Future consideration of possible examples should attempt to distinguish between selection which maintains unaltered the original

differences, if any (Grant, 1966b), between the species when they establish contact (i.e. a form of stabilising selection), and selection for greater similarity leading to actual convergence (convergent selection). In the absence of any indication of the latter, I suggest that the action of stabilising selection be invoked, as was done in the analysis of the *Thryothorus* wrens referred to above (Grant, 1966b).

#### CONCLUSIONS AND DISCUSSION

The principal conclusion to be drawn is that the evidence for the ecological aspect of morphological character displacement is weak. Several examples of supposed character displacement have been shown to be wrong or to be possibly correct but just as convincingly interpreted in other ways without recourse to character displacement (*Dendroica*, *Sitta*, *Puffinus*). Others illustrate the different but related principle of character release (*Geospiza*, *Acrocephalus*). Yet others are so complex that the unequivocal identification of character displacement is impossible, even though it may well have occurred (*Psittirostrinae*, *Anolis*).

The evidence is weak because the complexity of displacement patterns possible and the difficulties of obtaining unambiguous evidence have not been generally appreciated. The principal difficulties are:

- (1) Identifying original and derived populations.
- (2) Identifying pre-contact character states.
- (3) Predicting the character state in the zone of sympatry in the absence of character displacement.

The difficulties vary with the type of geographical situation. Islands have the advantage over mainland regions that the original and derived populations can be identified with some certainty. Some sympatric pairs of bird species on islands provide moderately good evidence of character displacement (*Parus*, *Centurus*, *Zosterops*). On the other hand islands suffer from the third difficulty more than do mainland regions. Islands that have no history of attachment to the mainland are the subject of an additional difficulty associated with sequential colonization. This is the problem of ascertaining how much of the character shift of the first colonist occurred prior to the arrival of the second colonist (e.g. Gill, 1971), and how much if any can be attributed to subsequent character displacement. Archipelagos are generally not good environments for seeking evidence of character displacement, except in the aggregate, because repeated colonization of each island by a species or its derivative and subsequent evolutionary change obscures the pattern of pre- and post-contact character states.

Evidence for the behavioural and ecological analogues of character displacement is more satisfactory because easier to obtain. Aggressive displacement of individuals of one species (of birds, ants, dragonflies, etc.) by individuals of another has been directly observed many times. The ecological consequence is that the former have been excluded from a feeding zone (Moore, 1964; Morse, 1967; Willis, 1966, 1968) or nesting habitat (Brian, 1956; Orians & Collier, 1963; Miller, 1968). Ecological displacement also occurs in the absence of aggression (De Bach, 1966).

In contrast to character displacement, the phenomenon of character release

has been documented quite extensively (e.g. Foster, 1964; Grant, 1965; Keast, 1968; Wilson, 1961). Again island-mainland comparisons yield most of the evidence because original and derived populations can be identified. However there is the difficulty here of separating the effects of the absence of a competitor in the island environment from the effects of a different array of environmental resources there (Grant, 1966a). So far, no single study has yet been able to separate these effects.

Furthermore, there is an abundance of evidence for the ecological analogue of character release. In allopatry, usually an island, a species occupies different or a greater variety of habitats, different or a greater range of feeding zones in a habitat, or reaches higher densities in a habitat, than in a region, usually mainland, where it is sympatric with presumed competitor species (Cameron, 1964; Corbet, 1964; Crowell, 1962, 1968; Cullen *et al.*, 1952; Diamond, 1970, 1971; Grant, 1965, 1966a, c, d; Keast, 1961, 1968; Lack, 1942, 1944; Lack & Southern, 1949; Marler & Boatman, 1951; Miller, 1951; Moreau & Ridpath, 1966; Svärdson, 1949; Volsøe, 1951, 1955; Williams, 1969). The role of a competitor species in facilitating the ecological release has been demonstrated experimentally in one situation, with voles and mice (Grant, 1969b, 1970, 1971a, b; Morris & Grant, 1972). However, in none of the cases of ecological release has the role of selection been demonstrated. It is perhaps unlikely, but all of the ecological release phenomena can be interpreted as purely "phenotypic" responses to the absence of competitor species.

It has often been assumed (e.g. Brown & Wilson, 1956) that character release is the "virtual image" of character displacement. But character release in allopatry does not necessarily imply that character displacement has occurred in sympatry. Instead, the large differences in character states between two species in sympatry may have been developed in allopatry, before the sympatry was established, and pre-adapted the species to sympatric existence. For example, the large differences in bill length between sympatric congeneric bird species on some islands are as much due to the fact that islands have been colonized to a disproportionate extent by the large and small members of the genus, as to evolution in the island environment (Grant, 1969a). Nevertheless the apparently frequent occurrence of character release does strongly suggest that character displacement has occurred, elsewhere, even if not necessarily in the same species which exhibit character release.

From the foregoing considerations, the second major conclusion is drawn; the likelihood of character displacement occurring is a function of the difference between the species, relative to the abundance and variety of the resources they exploit, at the time of initial contact. If the species are very similar they may compete severely. Selection will eliminate all members of one species that invades the range of the other. The minimum degree of difference between the two species necessary to permit sustained coexistence is too large for selection to produce by operating on initially near-identical species. Contiguous allopatry will be the usual resulting geographical distribution, and sympatry with interspecific territoriality an alternative (Grant, 1972b). On the other hand the species may be so different at the time of initial contact that the one does not appreciably influence the other's exploitation of resources, and extensive sympatry can be established without any noticeable character shifts attributable to the presence of the other species. Possibly most

coexistences have been established this way, without the occurrence of morphological character displacement. Where the difference between the character states of the two species at first contact is intermediate between these extreme conditions selection is likely to produce character displacement. It might not produce changes of large magnitude, contrary to the predictions of one model (Bossert, 1963; as quoted by Wilson, 1965), but rather somewhat fine adjustments to an environment holding a competitor species. If so, the detection of character displacement in its ecological aspect, particularly in mainland regions, will require a level of detail that has so far not been produced in a single study. It is therefore not surprising that the evidence for the ecological aspect of character displacement is at present so weak. This should be recognized and rectified.

#### ACKNOWLEDGEMENTS

The paper was written during a leave of absence at the Animal Ecology Research Group, Oxford, and I am grateful to Professor J. W. S. Pringle and Dr J. Phillipson for the provision of working facilities. I thank the many people who have discussed the subject with me, and I am particularly indebted to those who read part or all of the manuscript and who offered suggestions for its improvement: J. M. Anderson, N. P. Ashmole, G. A. Bell, W. Bock, W. R. P. Bourne, W. L. Brown Jr., A. J. Cain, M. L. Cody, L. Cornwallis, A. W. Diamond, M. P. Harris, A. K. Kepler, C. B. Kepler, D. Lack, B. K. McNab, D. H. Morse, T. W. Schoener, J. N. M. Smith and E. O. Wilson. Financial assistance was given by the National Research Council of Canada (Grant A2920).

#### REFERENCES

- AMADON, D., 1947. Ecology and the evolution of some Hawaiian birds. *Evolution, Lancaster, Pa.*, 1: 63-68.
- AMADON, D., 1950. The Hawaiian Honeycreepers (Aves, Drepaniidae). *Bull. Am. Mus. nat. Hist.*, 95: 155-262.
- AMADON, D., 1966. Insular adaptive radiation among birds. In Bowman, *The Galápagos. Proc. symp. Galápagos Internat. Sci. Project.* University of California Press.
- ASHMOLE, N. P., 1968. Body size, prey size, and ecological segregation in five sympatric tropical terns (Aves: Laridae). *Syst. Zool.*, 17: 292-304.
- BALDWIN, P. H., 1953. Annual cycle, environment and evolution in the Hawaiian honeycreepers. *Univ. Calif. Publs Zool.*, 52: 285-398.
- BETTS, M. M., 1955. The food of titmice in oak woodlands. *J. Anim. Ecol.*, 24: 283-323.
- BIRCH, L. C., 1960. The genetic factor in population ecology. *Am. Nat.*, 94: 5-24.
- BOCK, W., 1970. Microevolutionary sequences as a fundamental concept in macro-evolutionary models. *Evolution, Lancaster, Pa.*, 24: 704-722.
- BOSSERT, W. H., 1963. *Simulation of character displacement in animals*. Unpubl. Ph.D. thesis, Dept. of Applied Mathematics, Harvard University.
- BOURNE, W. R. P., 1955a. The Birds of the Cape Verde Islands. *Ibis*, 97: 508-556.
- BOURNE, W. R. P., 1955b. On the status and appearance of the races of Cory's Shearwater *Procellaria diomedea*. *Ibis*, 97: 145-149.
- BOURNE, W. R. P., 1957. Additional notes on the birds of the Cape Verde Islands, with particular reference to *Bulweria mollis* and *Fregata magnificens*. *Ibis*, 99: 182-190.
- BOURNE, W. R. P., 1963. A review of oceanic studies of the biology of seabirds. *Proc. 13th. Int. orn. Congr.*: 831-834.
- BOWMAN, R. I., 1961. Morphological differentiation and adaptation in the Galápagos Finches. *Univ. Calif. Publs Zool.*, 58: 1-302.
- BRIAN, M. V., 1956. Segregation of species of the ant genus *Myrmica*. *J. Anim. Ecol.*, 25: 319-337.
- BROWN, W. L., JR., 1958. General adaptation and evolution. *Syst. Zool.*, 7: 157-168.
- BROWN, W. L., JR., 1964. Two evolutionary terms. *Syst. Zool.*, 13: 50-52.

- BROWN, W. L., JR. & WILSON, E. O., 1956. Character displacement. *Syst. Zool.*, 5: 49-64.
- CAMERON, A. W., 1964. Competitive exclusion between the rodent genera *Microtus* and *Clethrionomys*. *Evolution, Lancaster, Pa.*, 18: 630-634.
- CHEKE, R. A., 1971. Feeding ecology and significance of interspecific territoriality of African montane sunbirds (Nectariniidae). *Revue Zool. Bot. afr.*, 84: 50-64.
- CODY, M. L., 1969. Convergent characteristics in sympatric populations: a possible relation to interspecific territoriality. *Condor*, 71: 222-239.
- CODY, M. L., 1970. Chilean bird distribution. *Ecology*, 51: 455-464.
- CODY, M. L. & BROWN, J. H., 1970. Character convergence in Mexican finches. *Evolution, Lancaster, Pa.*, 24: 304-310.
- CORBET, G. B., 1964. Regional variation in the bank-vole *Clethrionomys glareolus* in the British Isles. *Proc. zool. Soc. Lon.*, 143: 191-219.
- CROWELL, K. L., 1962. Reduced interspecific competition among the birds of Bermuda. *Ecology*, 43: 75-88.
- CROWELL, K. L., 1968. Competition between two West Indian flycatchers, *Elaenia*. *Auk*, 85: 265-286.
- CULLEN, J. M., GUITON, P. E., HORRIDGE, G. A. & PEIRSON, J., 1952. Birds on Palma and Gomera (Canary Islands). *Ibis*, 94: 68-84.
- DARWIN, C., 1859. *The origin of species*. London: Murray.
- DE BACH, P., 1966. The competitive displacement and coexistence principles. *A. Rev. Ent.*, 11: 183-212.
- DEEVEY, E. S., JR. & DEEVEY, G. B., 1971. The American species of *Eubosmina* Seligo (Crustacea, Cladocera). *Limnol. Oceanogr.*, 16: 201-218.
- DIAMOND, J. M., 1970a. Ecological consequences of island colonization by Southwest Pacific birds, I. Types of niche shifts. *Proc. natn. Acad. Sci. U.S.A.*, 67: 529-536.
- DIAMOND, J. M., 1970b. Ecological consequences of island colonization by Southwest Pacific birds, II. The effect of species diversity on total population density. *Proc. natn. Acad. Sci. U.S.A.*, 67: 1715-1721.
- FICKEN, R. W., FICKEN, M. S. & MORSE, D. H., 1968. Competition and character displacement in two sympatric pine-dwelling warblers (*Dendroica*, Parulidae). *Evolution, Lancaster, Pa.*, 22: 307-314.
- FOSTER, J. B., 1964. Evolution of mammals on islands. *Nature, Lond.*, 202: 234-235.
- GILL, F. B., 1971. Ecology and evolution of the sympatric Mascarene White-eyes, *Zosterops borbonica* and *Zosterops olivacea*. *Auk*, 88: 35-60.
- GRANT, P. R., 1965. The adaptive significance of some size trends in island birds. *Evolution, Lancaster, Pa.*, 19: 355-367.
- GRANT, P. R., 1966a. Ecological incompatibility of bird species on islands. *Am. Nat.*, 100: 451-462.
- GRANT, P. R., 1966b. The coexistence of two wren species of the genus *Thryothorus*. *Wilson Bull.*, 78: 266-278.
- GRANT, P. R., 1966c. The density of land birds on the Tres Marías Islands, Mexico, I. Numbers and biomass. *Can. J. Zool.*, 45: 391-400.
- GRANT, P. R., 1966d. The density of land birds on the Tres Marías Islands, Mexico, II. The distribution of species abundances. *Can. J. Zool.*, 45: 1023-1030.
- GRANT, P. R., 1968. Bill size, body size and the ecological adaptations of bird species to competitive situations on islands. *Syst. Zool.*, 17: 319-333.
- GRANT, P. R., 1969a. Colonisation of islands by ecologically dissimilar species of birds. *Can. J. Zool.*, 47: 41-43.
- GRANT, P. R., 1969b. Experimental studies of competitive interaction in a two-species system, I. *Microtus* and *Clethrionomys* species in enclosures. *Can. J. Zool.*, 47: 1059-1083.
- GRANT, P. R., 1970. Experimental studies of competitive interaction in a two-species system, II. The behaviour of *Microtus*, *Peromyscus* and *Clethrionomys* species. *Anim. Behav.*, 18: 411-426.
- GRANT, P. R., 1971a. Experimental studies of competitive interaction in a two-species system, III. *Microtus* and *Peromyscus* species in enclosures. *J. Anim. Ecol.*, 40: 323-350.
- GRANT, P. R., 1971b. The habitat preference of *Microtus pennsylvanicus*, and its relevance to the distribution of this species on islands. *J. Mammal.*, 52: 351-361.
- GRANT, P. R., 1972a. Bill dimensions of *Zosterops* species on Norfolk Island. *Syst. Zool.*, 21: (in press).
- GRANT, P. R., 1972b. Experimental studies of competitive interaction in a two-species system, V. Summary of the evidence for rodent species, and some theoretical considerations. *Ann. Rev. Ecol. Syst.*, 3: (in press).
- HALL, B. P., MOREAU, R. E. & GALBRAITH, I. C. J., 1966. Polymorphism and parallelism in the African bush-shrikes of the genus *Malacopteron* (including *Chlorophoneus*). *Ibis*, 108: 161-182.
- HARDIN, G., 1960. The competitive exclusion principle. *Science, N.Y.*, 131: 1292-1297.
- HESPENHEIDE, H. A., 1966. The selection of seed size by finches. *Wilson Bull.*, 78: 191-197.
- HESPENHEIDE, H. A., 1971. Food preference and the extent of overlap in some insectivorous birds, with special reference to the Tyrannidae. *Ibis*, 113: 59-72.
- HUTCHINSON, G. E., 1959. Homage to Santa Rosalia or Why are there so many kinds of animals? *Am. Nat.*, 93: 145-159.
- JACKSON, F. J., 1938. *The birds of Kenya Colony and the Uganda Protectorate*, 3. London: Gurney & Jackson.

- JAMES, F. C., 1970. Geographic size variation in birds and its relationship to climate. *Ecology*, 51: 365-390.
- KEAR, J., 1962. Food selection in finches, with special reference to interspecific differences. *Proc. zool. Soc. Lond.*, 138: 163-204.
- KEAST, A., 1961. Bird speciation on the Australian continent. *Bull. Mus. comp. Zool., Harv.*, 123: 307-495.
- KEAST, A., 1968. Competitive interactions and the evolution of ecological niches as illustrated by the Australian Honeyeater genus *Melithreptus* (Meliphagidae). *Evolution, Lancaster, Pa.*, 22: 762-784.
- LACK, D., 1942. Ecological features of the bird faunas of British small islands. *J. Anim. Ecol.*, 11: 9-36.
- LACK, D., 1944. Ecological aspects of species-formation in passerine birds. *Ibis*, 86: 260-286.
- LACK, D., 1945. The Galapagos Finches (Geospizinae). *Occ. Pap. Calif. Acad. Sci.*, 21: 1-159.
- LACK, D., 1947. *Darwin's Finches*. Cambridge University Press.
- LACK, D., 1971. *Ecological isolation in birds*. Oxford: Blackwell.
- LACK, D. & SOUTHERN, H. N., 1949. Birds on Tenerife. *Ibis*, 91: 609-626.
- LANYON, W. E., 1957. The comparative biology of the meadowlarks (*Sturnella*) in Wisconsin. *Nuttall Ornithological Club Publs.*, No. 1.
- LEVIN, D. A., 1970. Reinforcement of reproductive isolation: plants versus animals. *Am. Nat.*, 104: 571-581.
- MacARTHUR, R. H., 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology*, 39: 599-619.
- MacARTHUR, R. H. & LEVINS, R., 1964. Competition, habitat selection and character displacement in a patchy environment. *Proc. natn. Acad. Sci. U.S.A.*, 51: 1207-1210.
- MacARTHUR, R. H. & LEVINS, R., 1967. The limiting similarity of coexisting species. *Am. Nat.*, 100: 603-609.
- MacARTHUR, R. H. & WILSON, E. O., 1967. *The theory of island biogeography*. Princeton University Press.
- MARLER, P. & BOATMAN, D. J., 1951. Observations on the birds of Pico, Azores. *Ibis*, 93: 90-99.
- MAYR, E., 1963. *Animal species and evolution*. Cambridge, Massachusetts: Belknap Press of Harvard University.
- MCNAB, B. K., 1971. On the ecological significance of Bergmann's rule. *Ecology*, 52: 845-854.
- MILLER, A. H., 1951. A comparison of the avifaunas of Santa Cruz and Santa Rosa islands, California. *Condor*, 53: 117-123.
- MILLER, R. S., 1968. Conditions of competition between Redwings and Yellow-headed Blackbirds. *J. Anim. Ecol.*, 37: 43-62.
- MOORE, N. W., 1964. Intra- and inter-specific competition among dragonflies. *J. Anim. Ecol.*, 22: 253-273.
- MOREAU, R. E. & RIDPATH, M. G., 1966. The birds of Tasmania; ecology and evolution. *Ibis*, 108: 348-393.
- MORRIS, D., 1955. The seed preferences of certain finches under controlled conditions. *Avicult. Mag.*, 61: 271-287.
- MORRIS, R. D. & GRANT, P. R., 1972. Experimental studies of competitive interaction in a two-species system, IV. *Microtus* and *Clethrionomys* species in a single enclosure. *J. Anim. Ecol.*, 41: 275-290.
- MORSE, D. H., 1967. Foraging relationships of Brown-headed Nuthatches and Pine Warblers. *Ecology*, 48: 94-103.
- MURPHY, R. C., 1938. The need of insular exploration as illustrated by birds. *Science, N.Y.*, 88: 533-539.
- NØRREVANG, A., 1959. Double invasions and character displacement. *Vidensk. Meddr. dansk naturh. Foren.*, 121: 171-180.
- NORTH, A. J., 1904. Ornithological notes. *Rec. Aust. Mus.*, 5: 337-338.
- ORIANS, G. M. & COLLIER, C., 1963. Competition and blackbird social systems. *Evolution, Lancaster, Pa.*, 17: 449-459.
- ORIANS, G. H. & WILSON, M. F., 1964. Interspecific territories of birds. *Ecology*, 45: 736-745.
- PALMER, R. S., 1962. *Handbook of North American birds*, I. New Haven, Connecticut: Yale University Press.
- PARKES, K. S., 1965. Character displacement in some Philippine cuckoos. *The Living Bird. 4th Annual Report of the Cornell Laboratory of Ornithology*: 89-98.
- RIPLEY, S. D., 1959. Character displacement in Indian nuthatches (*Sitta*). *Postilla, No. 42*: 1-11.
- ROSENZWEIG, M. L., 1968. The strategy of body size in mammalian carnivores. *Am. Midl. Nat.*, 80: 299-315.
- SCHAFFER, W. M., 1968. Character displacement and the evolution of the Hominidae. *Am. Nat.*, 102: 559-571.
- SCHOENER, T. W., 1965. The evolution of bill size differences among sympatric congeneric species of birds. *Evolution, Lancaster, Pa.*, 19: 189-213.
- SCHOENER, T. W., 1967. The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. *Science, N.Y.*, 155: 474-477.

- SCHOENER, T. W., 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology*, 49: 704-726.
- SCHOENER, T. W., 1969a. Models of optimal size for solitary predators. *Am. Nat.*, 103: 277-313.
- SCHOENER, T. W., 1969b. Size patterns in West Indian *Anolis* lizards: I. Size and species diversity. *Syst. Zool.*, 18: 386-401.
- SCHOENER, T. W., 1970. Size patterns in West Indian *Anolis* lizards: II. Correlations with the sizes of particular sympatric species—displacement and convergence. *Am. Nat.*, 104: 155-174.
- SCHOENER, T. W. & GORMAN, G. C., 1968. Some niche differences among three species of lesser Antillean anoles. *Ecology*, 49: 819-830.
- SELANDER, R. K., 1966. Sexual dimorphism and differential niche utilisation in birds. *Condor*, 68: 113-151.
- SELANDER, R. K. & GILLER, D. R., 1963. Species limits in the woodpecker genus *Centurus* (Aves). *Bull. Am. Mus. nat. Hist.*, 124: 217-273.
- SMITH, N. G., 1966. Evolution of some Arctic gulls (*Larus*); an experimental study of isolating mechanisms. *Ornithological Monogr. No. 4*, American Ornithologist's Union.
- SOULÉ, M., 1966. Trends in the insular radiation of a lizard. *Am. Nat.*, 100: 47-64.
- SVÄRDSON, G., 1949. Competition and habitat selection in birds. *Oikos*, 1: 156-174.
- VAURIE, C., 1950. Notes on some Asiatic Nuthatches and Creepers. *Am. Mus. Novit.*, No. 1472: 1-29.
- VAURIE, C., 1951. Adaptive differences between two sympatric species of Nuthatches (*Sitta*). *Proc. Tenth Int. orn. Congr.*: 163-166.
- VOLSEN, H., 1951. The breeding birds of the Canary Islands, I. Introduction and synopsis of the species. *Vidensk. Meddr dansk naturh. Foren.*, 113: 1-153.
- VOLSEN, H., 1955. The breeding birds of the Canary Islands, II. Origin and history of the Canarian avifauna. *Vidensk. Meddr dansk naturh. Foren.*, 117: 117-178.
- WARNER, R. E., 1968. The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. *Condor*, 70: 101-120.
- WILLIAMS, E. E., 1969. The ecology of colonisation as seen in the zoogeography of anoline lizards of small islands. *Q. Rev. Biol.*, 44: 345-389.
- WILLIS, E. O., 1966. Interspecific competition and the foraging behaviour of Plain-brown Woodcreepers. *Ecology*, 47: 667-672.
- WILLIS, E. O., 1968. Taxonomy and behaviour of Pale-faced Antbirds. *Auk*, 85: 253-264.
- WILSON, E. O., 1956. Character displacement and species criteria. *Proc. Tenth Int. Congr. Entomol.*, 1: 125-128.
- WILSON, E. O., 1961. The nature of the taxon cycle in the Melanesian ant fauna. *Am. Nat.*, 95: 169-193.
- WILSON, E. O., 1965. The challenge from related species. In Baker & Stebbins, *The genetics of colonising species*. New York: Academic Press.
- WILSON, E. O. & BROWN, W. L., JR., 1955. Revisionary notes on the *sanguinea* and *neogagates* groups of the ant genus *Formica*. *Psyche*, 62: 108-129.