

RESOURCE SELECTION FUNCTIONS AND THE CONSERVATION OF ENDANGERED INVERTEBRATES

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Abstract: Resource selection functions (RSF) have been used successfully to establish the habitat requirements of vertebrates, but are less frequently used for invertebrates. The use of these functions with invertebrate species requires different sampling procedures and may be confounded by taxonomic status. In this study the presence and absence of habitat variables for the scarab beetle *Prodontria modesta* Broun were recorded in Central Otago, New Zealand. However, contrasting capture probabilities for isolated populations at sites with similar habitat variables confounded the RSF and the model did not converge. As the taxonomic status of *P. modesta* had recently been changed, morphology was checked for taxonomic distinctiveness. Consistent differences were found between two of the populations under study. The third population appeared to be a hybrid. This result gives support for the rationale behind RSF studies and provides evidence towards the major assumption of RSF being considered an 'if and only if' statement. Not only is it valid to calculate a RSF assuming a particular species will select the best out of the available options, but it is also valid to assume that when a RSF cannot be calculated (given sufficient data) that there may not be a single species/ecotype selecting.

Key words: insect conservation, scarab beetle, *Prodontria*, resource selection, New Zealand

Invertebrate conservation has a low profile in comparison to the charismatic vertebrates, e.g. bears, whales, dolphins and birds. The scale of the problem is different. Estimates in the late 1980's suggested that one quarter of the species of invertebrates on earth could disappear in the next 30-40 years, and the majority of these would not even have received a scientific name. Small-scale changes in ecosystems may have very little impact on large vertebrates but may result in the total extermination of an invertebrate species. Within large areas any given invertebrate species may only be able to survive in small patches with a particular topography, microclimate or biotic association (New, 1995). Consequently, work on endangered invertebrates is often hampered by a lack of data as they can be difficult to locate, and after they have been located, it may be difficult to isolate and quantify the important features of the habitat that allow the animal to persist in a particular patch. Resource selection functions have been successfully used to provide useful information in defining the habitat requirements of vertebrates (Boyce and Mc Donald, 1999) but this approach has been used less frequently for the conservation of invertebrates.

Different approaches to sampling the used and available habitats are necessary for flightless endangered invertebrates compared to the approaches used for mobile species. The situation is no longer one in which an animal has sampled and selected from available resource units. Instead, the endangered invertebrate has become marooned on a terrestrial island or patch, and the twin elements of habitat loss and increasing fragmentation of habitat patches (terrestrial islands) contribute to its decline (New, 1995). If a population is confined to a terrestrial island, we must assume that the island is the selected habitat as the population has been able to persist at this site. Likewise, we must assume that the habitat immediately surrounding the island is the unused but available habitat. Otherwise, logically the population would have either persisted in those areas or spread to them. However, we cannot assume that habitat further away from the terrestrial island is available as the invertebrate may not have access to these sites. Jamieson and Manly (1997) successfully used this approach to isolate the important habitat variables for the flightless grasshopper (*Sigaus childi* Jamieson). The presence or absence of habitat features, prominent at ground level, at sites with and without grasshoppers, was recorded. When they analyzed these data using a resource selection function they found the presence of a native cushion plant and small native herbs were very significant, as well as the requirement for 50% bare ground and an exposed site. Later, they were able to confirm their results with a transect survey in which 23 sites at 0.5km apart were scored. This work led to the identification and conservation of a large area of suitable habitat for this species.

Taxonomic status is of central importance for the conservation of endangered invertebrates, but is not usually of such importance with vertebrates. Invertebrates frequently hybridize when human induced habitat modification breaks down ecological boundaries (Rhymer and Simberloff, 1996). Taxonomic status therefore has the potential to confound resource selection studies as different species and/or ecotypes would be expected to have different patterns of use. The major assumption in any RSF study is that 'a species will select resources that are best able to satisfy its life requirements and that high quality resources will be selected more often than low quality' (Manly et al, 2002). Therefore, when similar resources are available in different areas we would expect there to be similar patterns of use. If this assumption is violated then the whole rationale for RSF studies becomes suspect unless we can find a

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valid cause. In this paper the habitat requirements of the chafer beetle *Prodontria modesta* are studied. This species replaced two species, *Prodontria modesta* and *Prodontria bicolorata* (Given, 1952), which were formally synonymized by Emerson and Barratt (1997). If the synonymization was valid, we would expect similar patterns of habitat use by different populations of this species when similar resources are available.

STUDY AREA

Alexandra is at the center of Central Otago, the dry interior of southern New Zealand (Fig. 1). It has a continental climate with low rainfall (358mm), hot summers (mean maximum 24°C) and cold winters (mean maximum 8°C) (Johnson, 1986). The district is situated around the junction of the Clutha and Manuherikia Rivers and is part of an extensive lowland bounded by schist-mountains (McCraw, 1964). The three study sites were all within a 10-Km radius of Alexandra but were isolated from each other by the rivers. Crawford Hills is primarily pasture used for sheep farming, the Conroy's Dam site included orchards, vineyards and pasture, and the Airport site is mixed pasture broken by sand and gravel. All sites have large areas covered with the invasive plant *Thymus vulgaris*, as well as pockets of native vegetation dominated by the cushion plant *Raoulia australis*.



Fig. 1 Site map.

METHODS

Presence or absence of substrate and biological habitat features at 27 sites (Table 1) chosen at random among major vegetation types near Alexandra in Central Otago, New Zealand were recorded. At each site 5 pitfall traps (9cm diameter, 8.5cm deep) with 4 – 5 cm of soil in the bottom were put out in rough circles, approximately 2m apart, on the circumference of a circle (diameter 3m). On two occasions traps were placed in a line, as there was insufficient area for the normal sampling.

Pitfall traps were checked at 7-day intervals \pm 1 day for beetles over a 10-week period (9 Oct-12 Dec 1997) during which adult beetles are known to be active, and the numbers of beetles captured were recorded. Capture probabilities were calculated from the presence of beetles in a trap group (i.e. 5 traps combined) per week. Traps were out for varying lengths of time (Table 2) as some trial traps were put in place initially and therefore had a longer sampling period, while at other sites nothing was ever caught and traps were removed after a few weeks and repositioned elsewhere. Any beetles found alive (<10%) were released at least 2m away from the pitfall trap area, or if dead were retained and either stored frozen, or mounted and dried. Trap sites where beetles survived were usually heavily populated, and the few released beetles would not have changed site capture probabilities.

A logistic regression of beetle presence and absence related to habitat features was carried out to isolate the important habitat variables necessary for the persistence of the species in an area. However, as totally opposite patterns of use were found at Airport and Crawford Hills, it was obvious that this procedure would not produce meaningful results. There were insufficient sites within each locality to attempt separate logistic regressions.

Basically the data disagreed with the major assumption of resource selection, that a species will select the same resources to satisfy its life requirements given similar availability. Instead of abandoning the RSF approach, data were critically examined to find a cause for this result. First, a cluster analysis of habitat features was carried out to confirm the visual impression that sites at Crawford Hills and Airport were very similar. To simplify the cluster analysis, sites at Conroy's Dam were excluded as they were quite different from sites at the Airport and Crawford Hills, and there was no point in comparing capture probabilities at these sites. Euclidean distance and Ward's linkage were used in a hierarchical cluster analysis as this combination of distance and linkage methods are reputed to produce the most interpretable results. Both procedures were carried out with Minitab (1994).

One possible explanation for the confounding of the RSF was the species status of the beetle populations at Crawford Hills and Airport. These two populations were considered separate species (*P. modesta* and *P. bicolorata*) before being formally synonymized by Emerson and Barratt (1997). Identification of the *Prodontria* genus is based on the structure of the male genitalia and the antennae (Emerson and Barratt, 1997). The morphology of the antennae and details of the male genitalia were examined with the aid of an Olympus dissecting microscope and drawings were made using an eyepiece graticule. An outline of the male genitalia was drawn from a strict lateral view to show differences among population-based types. Measurements of male genitalia were made from 1:40 scale drawings. Another possible explanation is that the real variables related to selection were not measured but this seemed unlikely as habitat variables typical for scarab beetles were measured.

RESULTS

Capture Probabilities

The logistic regression relating beetle presence and absence to habitat variables did not converge, and no variable was significant in univariate models. The model was confounded by two quite different responses with respect to population. Converse capture probabilities were found for similar sites which were characterized by predominantly pasture grasses, at Crawford Hills (3, 5 and 6) and Airport (7, 10 & 11) (Tables 1 and 2). At Crawford Hills the mean probability of capture was $P = 0.95$ (for sites 3, 5 and 6), whereas at Airport the mean probability of capture was $P = 0.20$ (for sites 7, 10 and 11). The similarity of these sites was confirmed by cluster analysis (Fig. 2). The highest probability of beetle capture at Airport was at sites 8, 9, 12 and 13, which were mainly loose sand and gravel with little plant cover. Sites with soil (as compared to sand) and covered with thyme (16 and 17) had very low probabilities of capture. No beetles were found at sites under pine trees (14 and 15). In contrast, Crawford Hills sites with established pasture (3, 4 and 5) had high probabilities of beetle capture, but none were caught at an irrigated site (1). One beetle was caught at a salty site (2). Beetles appeared to be numerous in the Crawford Hills generally and attracted the attention of members of the public. At Conroy's Dam beetles were found only at a site with the native cushion plant *R. australis* (22). No beetles were found at a site in an orchard with established pasture (20) or at roadside sites (18, 19, and 21). However, only four types of habitat were sampled in this area, as other habitat types were well represented elsewhere.

Morphology

Outlines of the male beetles' genitalia (Fig. 3) from Crawford Hills and Airport populations are shown. There are consistent differences in shape between Crawford Hills and Airport populations. The Airport population has a distinctive shoulder emerging from the neck of the basal shield which is not found in the Crawford Hills population. The lengths of the basal shield differed significantly between the populations (Student's t-test, $t = 3.1$, $df = 8$, $p < 0.01$) but the lengths of the claspers were not significantly different. The shape of the male genitalia of the Conroy's Dam population (not shown) is variable and exhibits characters found in both Crawford Hills and Airport populations. One individual examined resembled individuals from the Crawford Hills population when viewed from one side, but resembled individuals from the Airport population from the other side. Differences were also found between the antennae of Crawford Hills and Airport populations. The length of the lamellae and the antennal club varied within each population, but the 3 – dimensional angles of the antennae varied considerably and consistently between the populations (Fig. 4). Both populations were similar from a lateral view, but when the antennae were rotated 90° differences can be seen in the angle the second segment makes with the first segment. This difference is found in both males and females, and is necessary to accommodate a difference in the shape of the base of the maxillae. Both types were found in the Conroy's Dam population.

Table 2. Pitfall trap sites, site number, capture probabilities (P), length of time sampled and total number of beetles caught per site (n).

area	Site #	P	weeks	n
Crawford Hills	1	0.0	5	0
Crawford Hills	2	0.2	5	1
Crawford Hills	3	0.9	10	18
Crawford Hills	4	1.0	10	38
Crawford Hills	5	0.9	10	31
Crawford Hills	6	1.0	10	27
Airport	7	0.2	10	3
Airport	8	0.8	10	34
Airport	9	0.88	8	20
Airport	10	0.25	8	3
Airport	11	0.13	8	1
Airport	12	1.00	8	27
Airport	13	1.00	8	34
Airport	14	0.00	8	0
Airport	15	0.13	8	1
Airport	16	0.13	8	1
Airport	17	0.00	8	0
Conroy's Dam	18	0.00	3	0
Conroy's Dam	19	0.00	3	0
Conroy's Dam	20	0.00	3	0
Conroy's Dam	21	1.00	4	15
Conroy's Dam	22	0.86	7	20
Conroy's Dam	23	0.86	7	21
Conroy's Dam	24	1.00	7	40
Conroy's Dam	25	1.00	7	34
Conroy's Dam	26	1.00	7	89
Conroy's Dam	27	0.86	7	42

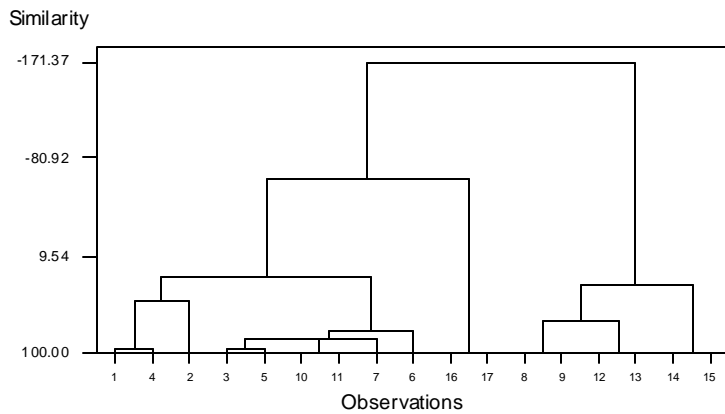


Fig. 2 Cluster analysis using squared Euclidean distance and Ward's method of linkage.

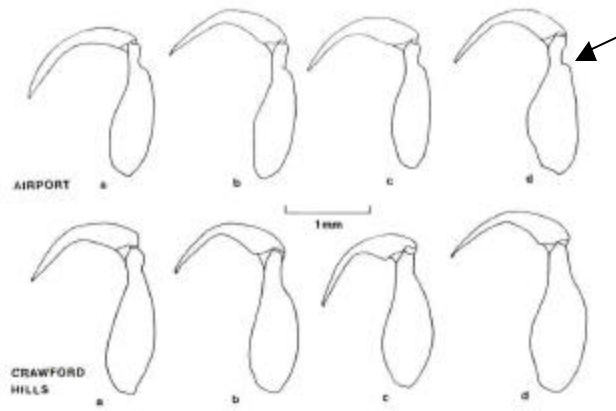


Fig. 3 Outline of male genitalia, (distinctive shoulder shown with arrow).

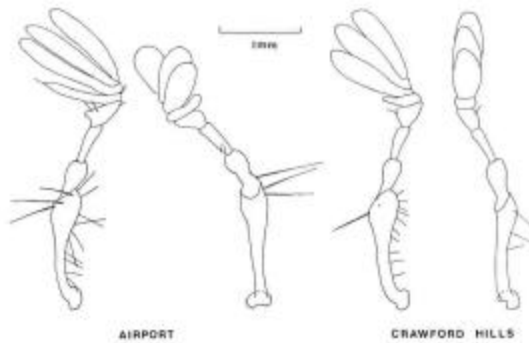


Fig. 4 Outline of antennae. The angle between the base and the top of the antenna is greater in the Airport population than in the Crawford Hills population, to accommodate a difference in the structure of the mandible.

DISCUSSION

The analysis of resource selection data indicated a contrasting response by *Prodontria* beetles to habitat variables at Airport and Crawford Hills sites. Under the prevailing hypothesis that *P. modesta* is a widespread generalist species (Emerson and Wallis, 1994) this result could be ascribed to patchy distributions, but this seemed unlikely as the probability of beetle capture in sandy ground directly alongside the grassy area at the Airport was very high ($P = 0.84$). Therefore, although pasture habitat was directly available to large numbers of beetles at the Airport it was avoided, whereas at Crawford Hills the highest numbers of beetles were found at sites with pasture grasses. Also, the idea of a patchy distribution contradicts our notion of a generalist being tolerant and widespread. An alternative explanation for these contradictory results would be if the beetle populations found at Crawford Hills and at Airport were different species. A morphological analysis of beetles from the Crawford Hills and Airport populations showed they varied significantly and consistently, in the structure of the male genitalia and in the structure of the male and female antennae. These structures are still used for distinguishing between species of scarab beetle (Emerson and Barratt, 1997).

At Conroy's Dam, beetles were found continuously distributed in areas dominated by *R. australis*, but were not found in other areas. Structural differences were not as consistent as for the other populations. For example, male

genitalia exhibited characteristics from both populations, but usually the *P. modesta* form dominated. The ratio of dark:light forms (dark including all individuals which could be distinguished from the two-tone light form) in randomly collected sample of 60 gave a classic Mendelian ratio 3:1 (44:16). This suggests a stable color polymorphism (Roff, 1996) and a freely interbreeding population. This result is in agreement with the allozyme analysis by Emerson and Wallis (1994) in which they found both color forms at Conroy's Dam had the same allozymes. Porter and Rust (1997) had good agreement between allozymes and morphology in their study on the phylogenetic relationships among North American scarab beetles.

Overall the results of this study are contrary to the thesis of Emerson and Wallis (1994) who suggested the species distinction between *P. modesta* (in the Alexandra area) and *P. bicolorata* (the Airport population) was not justified. These totally contrary conclusions are understandable if the design of their study is considered. Basing their study on the biological species concept (BSC), they examined the morphological variation between the two color variants in 'sympatric populations to avoid population differences confounding this result' e.g. Conroy's Dam. Species status was made solely on the basis of external color. All dark colored individuals were assigned to *P. modesta* and all light colored individuals to *P. bicolorata*. They also noted 'interspecific mating' occurred between the two color variants in the field, and that individuals of intermediate color could be found in their 'sympatric populations'. From these data they concluded that they had one species in the Alexandra area. An alternative hypothesis is that the 'sympatric populations' are hybrid populations. This would allow for 'interspecific mating' and similar allozymes within one population. It would also explain the inconsistent morphological features, which are typical of hybrid populations (Rhymer and Simberloff, 1996).

Under the BSC, failure to find a barrier to gene flow in sympatry usually implies conspecificity, but this is also acknowledged as one of the deficiencies of the BSC (Erhlich, 1961). Often isolating mechanisms are only present when species have evolved sympatrically or parapatrically, but not allopatrically. For example, Sperling *et al* (1997) showed that most crosses of six allopatric species of *Limnosporus* water striders hybridized easily in the laboratory. The loss of alleles through hybridization and introgression is now a well established phenomenon and can be especially problematic for rare species coming into contact with more abundant ones (Rhymer and Simberloff, 1996). Introduced species are usually proposed as the culprits for this type of extinction, but habitat modification can also break down reproductive isolation between native species with subsequent mixing of gene pools (Rhymer and Simberloff, 1996).

The Alexandra area of New Zealand has numerous fault lines. Land movements may have been responsible for bringing *Prodontria* beetles alongside each other, and when followed by habitat degradation, physical boundaries associated with ecological preferences would be removed and allow interbreeding. Soil maps of the Alexandra region (McCraw, 1964) indicate that regions where the *P. bicolorata* form and the hypothesized hybrid zone at Conroy's Dam are found correspond to regions where the soil is predominantly Lowburn sands. The largest area of Lowburn sands is at the Airport and smaller pockets are found at Crawford Hills and Conroy's Dam. These regions are surrounded by soils of different origins. The Airport population of the *P. bicolorata* form is confined to loose sandy habitat which suggests it is a remnant population of a *Prodontria* species associated with the Lowburn sands. At Crawford Hills, the *P. modesta* form tolerates habitat modifications resulting from agriculture, which suggests it may have been associated with a different substrate, as it is tolerant of the build up and consolidation of soil. The proposed hybrid population at Conroy's Dam requires further research. Initial differences in founder populations and genetic isolation (the three populations are separated by rivers) would explain the high degree of genetic variation between the populations observed by Emerson and Wallis (1994).

Under the phylogenetic species concept (Cracraft, 1983) the Airport and Crawford Hills populations are separate species as morphological characters are fixed and unique. Also, the restriction of the *P. bicolorata* form to a particular type of habitat is a unique ecological character. Structural differences between the *P. modesta* form and the *P. bicolorata* should be maintained through selection on color varieties provided habitat is conserved. A lighter color would be more adaptive on light sandy substrates whereas a dark color is more adaptive for darker substrates. If the species status of the *P. bicolorata* form is ignored there will be a significant loss of biodiversity. For example, if the number of presumptive alleles for 7 loci identified by Emerson and Wallis (1994) in their allozyme study is compared among the populations, both the Crawford Hills and Conroy's Dam populations have 25% fewer alleles than the Airport population. This suggests that the conservation priorities of the recently synonymized *P. modesta* must change. The re-establishment of *P. bicolorata* as a separate species and its conservation is necessary. Also, it is important that hybrid populations are treated as separate entities at least until their conservation requirements are known.

Although this study did not result in the calculation of a resource selection function, it does highlight the usefulness of the data collected in such studies. It is unlikely that the differences between these populations would have been re-acknowledged if the RSF approach had not been taken. The U. S. Endangered species Act identifies

and protects endangered and threatened species, subspecies and populations (Haig, 1998). This method could be useful to identify significant ecological variants and to establish legally sustainable habitat requirements for endangered invertebrates. New (1995) suggested that the most tangible way to understand the habitat needs for animals or plants is through the study of the organisms themselves, but resource selection studies provide a viable quick alternative.

This study also gives support for the rationale behind RSF studies and provides evidence towards the major assumption of RSF studies being considered an 'if and only if' statement. That is, either both parts of the statement (calculating a valid RSF and one species selecting) are true or both are false. Thus, we can calculate a RSF assuming one species will select the best out of the available options, but we cannot calculate a RSF when there is more than one species/ecotype selecting. If this result was found to be widely applicable it could have considerable application in the conservation of invertebrates, as it would speed up the recognition of new species and their habitat requirements. Further empirical work is needed in this area.

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