Journal of Biogeography (1982) **9**,391–396

The effect of habitat utilization on species–area curves: implications for optimal reserve area

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ABSTRACT. The biological reserves in the wheatbelt of Western Australia form islands of native vegetation in a sea of arable farmland. Subdivision of the species in three vertebrate taxa (mammals, passerine birds and lizards) into species retained only in reserves (*u* species) and those also surviving outside the reserves in disturbed areas (*d* species) show conflicting requirements for reserve area.

In each taxon *u* species are lost disproportionately with a reduction in area. The *d* species are favoured by more smaller reserves while *u* species, those most in need of conservation, are favoured by larger reserves.

Introduction

The conservation of species is increasingly dependent on the creation of biological reserves. Within the constraints of available land resources the decision on whether to create one large reserve or several smaller ones of equal total area has become a contentious issue (Terborgh, 1974; Diamond, 1975; May, 1975; Simberloff & Abele, 1976).

The number of species (S) contained in an area (A) is generally described by an equation of the form $S = CA^z$ where C and z are positive constants with $1 > z > 0$. Hence it is argued that larger areas should be reserved as they will contain more species. Alternatively it is argued that while two smaller areas will each contain less species than one larger area, because all species are not common to the two areas the reservation of the two smaller areas will contain more individual species. This controversy has recently been the subject of theoretical and empirical analyses which have shown that a number of smaller reserves contain more individual species than fewer larger reserves of the same combined area (Gilpen & Diamond, 1980; Higgs & Usher, 1980) but that excessive subdivision may become suboptimal (Gilpen & Diamond, 1980).

The wheatbelt of south western Western Australia contains numerous nature reserves of native vegetation while the remainder has mostly been cleared for arable agriculture; the reserves thus form islands of natural vegetation in a 'sea' of wheat. Intensive surveys of twenty-one nature reserves (34–5119 ha) (Kitchener *et al.*, 1980a, b, 1982) throughout the 140 000 km^2 wheatbelt have shown for the taxa considered (mammals, passerine birds and lizards) the number of species increased directly with increasing reserve area but at a decreasing rate (Table 1) as expected from both theoretical and empirical studies (Connor & McCoy, 1979).

The species present in each vertebrate order in the reserves were divided into two groups; those occurring only in the relatively undisturbed original vegetation (*u* species) represented by the reserves, and those (*d* species) which in addition live outside such areas in the disturbed or exotic vegetation represented by arable and pastoral farming, road verges, heavily grazed native vegetation

0305-0270/82/0900-0391 $02.00

TABLE 1. Statistics describing the relationship, in various taxa, between the number of species (S) and area (A ha) in equations of the form $S = C + z\ln A$ and, in parentheses, of the form $S = CA^z$

Taxa	Group*	C	z	r^2	F test; $P <$
Mammals	d	0.49 (0.99)	0.66 (0.23)	0.34 (0.40)	0.01 (0.005)
	u	−3.92 (0.02)	1.19 (0.79)	0.63 (0.38)	0.001 (0.005)
	$d + u$	−3.43 (0.97)	1.84 (0.32)	0.67 (0.69)	0.001 (0.001)
Passerine birds	d	12.10 (14.10)	2.55 (0.11)	0.43 (0.43)	0.005 (0.005)
	u	−5.92 (0.04)	2.28 (0.80)	0.68 (0.32)	0.001 (0.01)
	$d + u$	6.40 (13.15)	4.76 (0.16)	0.66 (0.62)	0.001 (0.001)
Lizards	d	1.31 (2.93)	1.07 (0.15)	0.37 (0.36)	0.005 (0.005)
	u	−5.05 (0.06)	2.36 (0.76)	0.56 (0.29)	0.001 (0.025)
	$d + u$	−3.74 (2.99)	3.43 (0.27)	0.57 (0.55)	0.001 (0.001)
All	d	15.05 (19.29)	4.18 (0.12)	0.49 (0.48)	0.001 (0.001)
	u	−14.88 (0.91)	5.82 (0.48)	0.81 (0.60)	0.001 (0.001)
	$d + u$	−0.91 (16.72)	10.10 (0.21)	0.74 (0.68)	0.001 (0.001)

* Group u species survive in areas of natural vegetation as represented by biological reserves. Group d species survive also in disturbed areas, e.g. arable and pastoral farmland, road verges and urban areas.

and urban areas. These categories have been detailed and used elsewhere (Kitchener *et al.*, 1980a, b, 1982; Kitchener, 1982).

Results

The species–area relationships for both d and u species are adequately described by both logarithmic ($S = C + z\ln A$) and power equations ($S = CA^z$) (where S = number of species in area A (ha), with C and z as constants) but the former gives a marginally better fit (Table 1).

In each order the proportion of u species of the total species ($u + d$ species) declines rapidly as the reserve area is reduced below ≃ 600 ha (Fig. 1a). Scaling the data (Figs. 1b–d) shows that the three orders respond similarly to changes in reserve size and that in each case the smaller reserves contain relatively more d species.

We examined the species overlap in all 231 possible pairs of the twenty-one reserves and compared the observed overlap with that expected from the species–area relationship ($S = CA^z$) using equation (5) in Higgs & Usher (1980) and derive the index S_0 = observed − expected species overlap. Values of $S_0 > 0$ indicate that for each reserve pair compared more species would have been retained with the reservation of one area equal to the combined area of the two reserves. Values of $S_0 < 0$ show species numbers were enhanced by the subdivision.

The distance (2–583 km) between the reserves we compared strongly influenced the index S_0 in three of the six categories (Table 2). In these three cases the regression equations were used to correct the index S_0 to zero distance so that comparisons could be made excluding the influence of distance between reserves. In Fig. 2 the frequency distribution of S_0 is presented for each of the six categories both corrected and uncorrected for distance effects. In each order more than 86% of the comparisons for u species have $S_0 > 0$ (mammals 95% $S_0 > 0$; passerines 86%

FIG. 1. The relationship between area (ha) and the proportion of d and u species in twenty-one nature reserves in the wheatbelt of Western Australia. (a) The lines of best fit are drawn after reconversion from regressions of the proportion (angular transformation) of u species of $u + d$ species on log area (or first order polynomial for reptiles); ——●——, mammals; ·····∗·····, passerine birds; —·—⊙—·—, lizards; ——, all species. (b–d) The proportion of d and u species of the number of each present in a reserve of 2000 ha (from Table 1) as the area is reduced. The curve with negative slope is the difference between the curves for d and u species and represents the relative excess of d species over u species compared with their distribution at 2000 ha; (b) mammals, (c) passerine birds, (d) lizards.

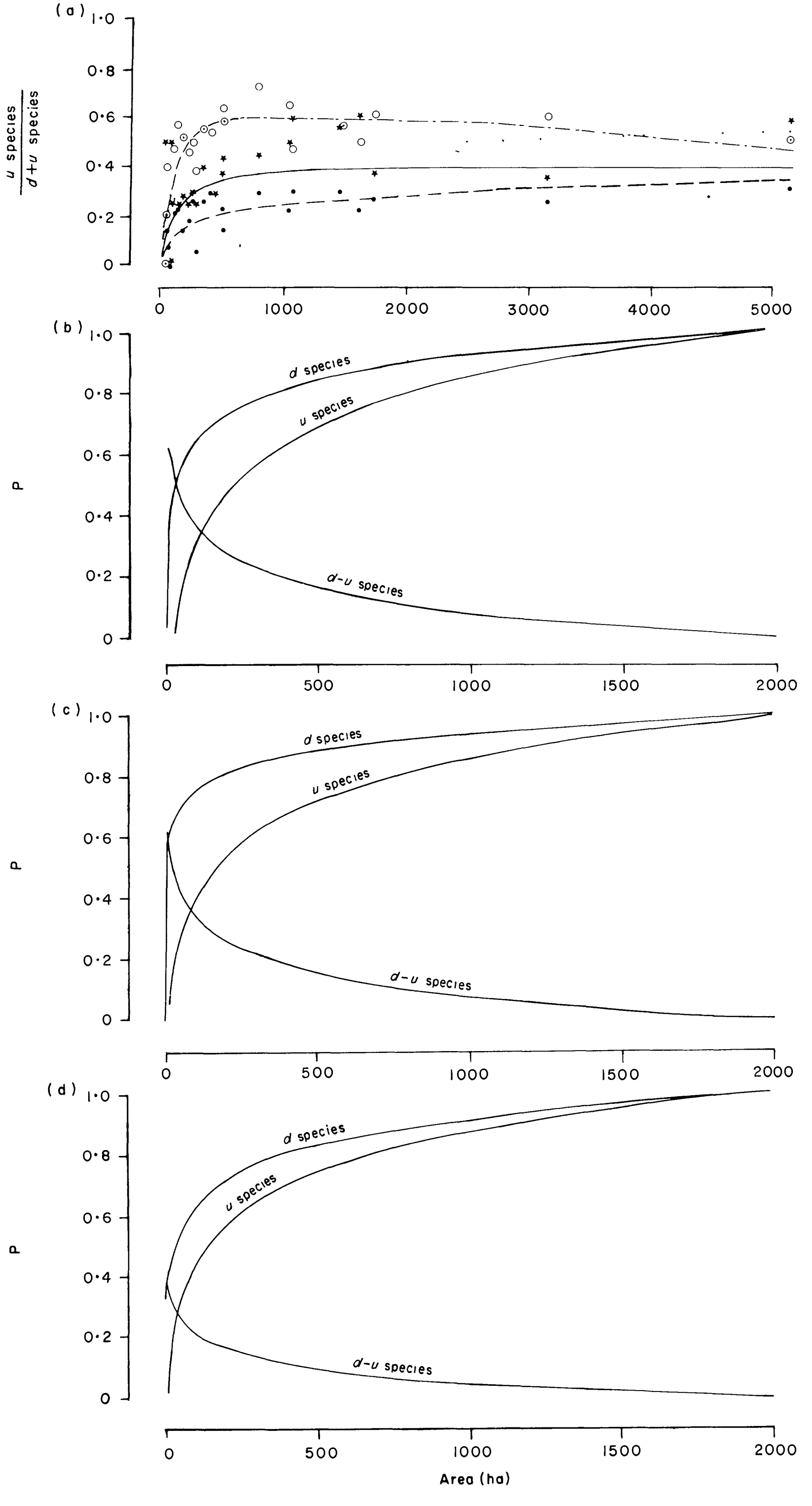
(a)
u species / d+u species
1·0
0·8
0·6
0·4
0·2
0
0
1000
2000
3000
4000
5000
(b)
P
d species
u species
d–u species
0
500
1000
1500
2000
(c)
P
d species
u species
d–u species
(d)
P
d species
u species
d–u species
Area (ha)

TABLE 2. Summary statistics comparing the frequency distribution of the index S_0 from zero (n = 231) and between d and u species in each order (N = 462). S_0 = observed – expected species overlap in paired comparisons of twenty-one reserves

Order	Category	t_s	Mean from zero	$\bar{x}S_0$	t_s	Between means
Mammals	d species	2.7	$P < 0.02$	<0	16.6	$P < 0.001$
	u species	20.6	$P < 0.001$	>0		
Passerines	d species	20.5	$P < 0.001$	<0	28.9	$P < 0.001$
	u species	16.7	$P < 0.001$	>0		
Lizards	d species	26.9	$P < 0.001$	<0	26.3	$P < 0.001$
	u species	18.1	$P < 0.001$	>0		

$S_0 > 0$; lizards 89% $S_0 > 0$). For d species in each order more than 61% of the paired comparisons show S_0 values < 0 (mammals 95% $S_0 < 0$; passerines 61% $S_0 < 0$; lizards 93% $S_0 < 0$). In each order the distribution of d and u species differ ($P < 0.001$) and all categories of u and d species have mean S_0 values respectively greater and less than zero ($P < 0.02$; Table 3). Hence in each order compared (Fig. 2; Table 3) on average more individual d species were present in the two reserves compared than would be expected from a single reserve of equal total area. In more than 86% of cases less u species were present in the two reserves than would be expected from one large reserve equal to their combined area.

Combining d and u species for analysis yields S_0 values close to zero (mammals S_0 = 1.3, passerines $S_0 = 0.3$, lizards $S_0 = -0.2$) giving the incorrect impression that reserve sizes are optimal.

The disproportionate change with area in species richness of d and u species leads to conflicting requirements between the two groups for optimal reserve size; u species are favoured by large reserves and d species by more smaller reserves. However, because nature reserves are primarily for u species and not d species (which can flourish in disturbed situations and are thus generally not endangered), the most appropriate reserve design is to set aside areas that are at least sufficiently large so that u species are not under-represented relative to d species.

For oceanic islands, theory (Gilpen & Diamond, 1980) and intuition suggest that small islands will not favour species with large area requirements. To date no empirical data have shown clearly that taxa can be subdivided on any criteria to produce statistically different distributions for their area requirements on continental habitat patches.

If this example from Western Australia is a general case it has important implications to one aspect of reserve design, namely how to make effective use of area available to ensure maximum retention of species. The use of species–area curves for entire taxa, without considering differential use of habitat by the species contained therein, may result in unexpectedly low richness of u species, the group most likely to be in need of conservation. In addition the identification of species groups which respond differently to habitat islands has important implications for the use

TABLE 3. Regression equations describing the relationship between the index S_0 (y) and the distance between reserves (x km; n = 231). Distances vary from 2 to 583 km.

Order	Category	Regression equation	r_s	P
Mammals	u species	$y = -0.076x + 30.54$	−0.45	<0.01
	d species	$y = 0.006x - 5.68$	0.04	NS
Passeries	u species	$y = -0.011x + 29.07$	−0.073	NS
	d species	$y = -0.00016x - 20.54$	−0.002	NS
Lizards	u species	$y = -0.036x + 16.12$	−0.35	<0.01
	d species	$y = -0.049x - 18.98$	−0.42	<0.01

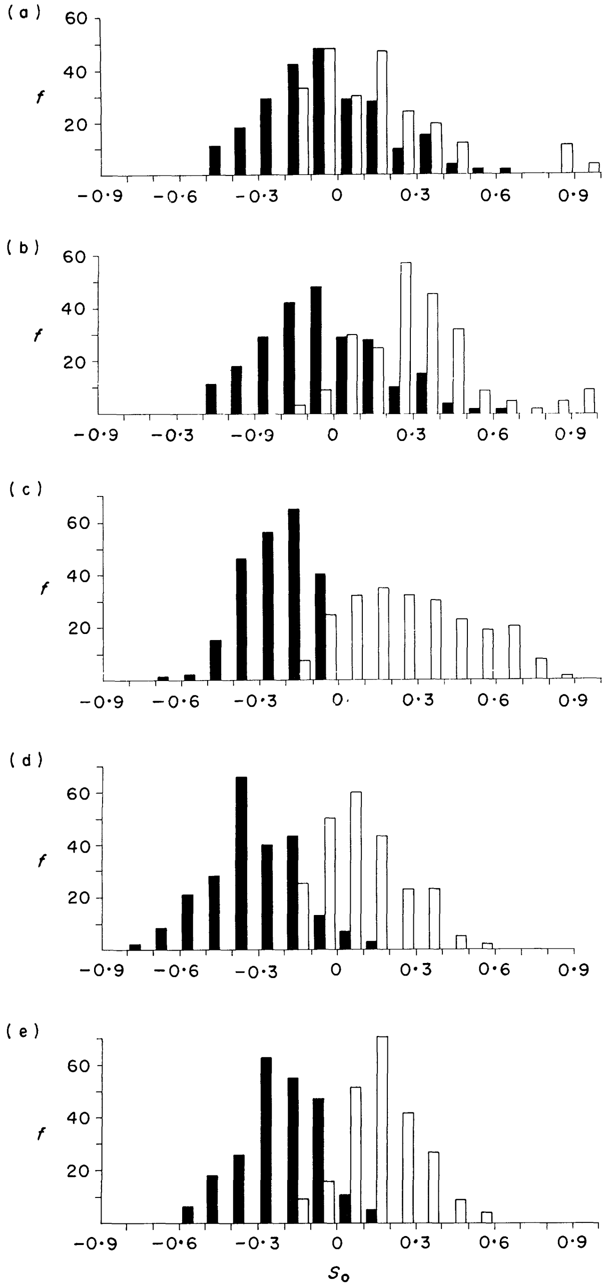

FIG. 2. Frequency distributions of observed–expected species overlap (S_0) of twenty-one nature reserves in the wheatbelt of Western Australia. Expected species overlap was calculated using equation (5) in Higgs & Usher (1980). If $S_0 > 0$ one large reserve, equal to the combined area of the two smaller reserves under comparison, would contain more individual species than the sum of species in the two smaller reserves; if $S_0 < 0$ vice versa. The values are calculated from the power equations in Table 1 and are presented uncorrected and, where necessary, corrected for the effect of the distance between reserves using equations in Table 2. Open bars: *u* species; solid bars: *d* species. (a) Mammals: uncorrected. (b) Mammals: *d* species corrected; *d* $\bar{x} = -0.40 \pm 2.28$; *u* $\bar{x} = 3.08 \pm 2.28$. (c) Passerine birds: correction unnecessary; *d* $\bar{x} = -1.99 \pm 1.47$; *u* $\bar{x} = 1.60 \pm 1.45$. (d) Lizards: uncorrected. (e) Lizards: *d* and *u* species corrected; *d* $\bar{x} = 2.24 \pm 1.25$; *u* $\bar{x} = 2.69 \pm 2.26$. Error bounds are ± 1 standard deviation, $n = 231$.

of islands of remnant vegetation to test biogeographic theory.

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