

TESTING FOR RESOURCE USE AND SELECTION BY MARINE BIRDS

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Abstract.—An unfamiliar yet easily computed statistical procedure for determining dietary, habitat or other resource preferences of marine birds is described. The technique tests for significant differences between individual categories of observed and expected frequency data. The procedure is illustrated by examining marine habitat preferences of Short-tailed Shearwaters (*Puffinus tenuirostris*) and dietary preferences of Crested Auklets (*Aethia cristatella*) in the northwestern Bering Sea, Alaska. Compared to other analytical approaches typically used during field investigations of marine birds, this technique has both practical and statistical qualities that favor its application, including: 1) robust and easily-met assumptions, 2) control of the experiment-wise error rate, 3) flexible response to unforeseen logistical and sampling problems that frequently arise at sea, 4) greater specificity for determining resource preferences and 5) results based directly on counts of birds rather than samples of line transects or some other arbitrary observation interval.

PRUEBAS PARA LA SELECCIÓN Y USO DE RECURSOS POR PARTE DE AVES MARINAS

Sinopsis.—Se describe un procedimiento estadístico para determinar preferencias en la dieta, habitat y el uso de otros recursos por parte de aves marinas. La técnica permite examinar para diferencias significativas la frecuencia de datos esperados y observados, arreglados en categorías individuales. El procedimiento es ilustrado examinando preferencias de habitat en individuos de *Puffinus tenuirostris* y preferencias en la dieta en individuos de *Aethia cristatella*, en la parte noroeste del Mar de Bering, Alaska. Al compararse esta técnica con las usualmente utilizadas para estudios en el campo de aves marinas, la misma tiene cualidades prácticas y estadísticas que favorecen su aplicación y que incluyen: 1) suposiciones robustas y fáciles de alcanzar, 2) control de la tasa de error experimental (wise-error), 3) respuesta flexible a problemas de muestreo que frecuentemente ocurren en el mar, 4) gran especificidad para determinar preferencia de recursos y 5) resultados basados directamente en censos de aves en vez de muestras de transectos lineales u otro tipo de observaciones a intervalos arbitrarios.

In the last two decades, studies of the marine ecology of seabirds have evolved rapidly from large-scale surveys (Brown 1980, Pocklington 1979) to more detailed investigations of underlying mechanisms and processes responsible for patterns of distribution and abundance (Briggs et al. 1987, Hunt and Schneider 1987). Concurrently, marine ornithologists have begun to scrutinize and question the most efficient analytical models, including inferential statistics, employed to complement analyses of their field surveys (e.g., Haney and Solow 1992, Schneider and Duffy 1985).

Here, we describe and apply a simple procedure based on Bonferroni's inequality for determining statistical associations between seabirds and marine resources. The method tests for differences in use of individual resource categories via comparisons between observed and expected proportions. We advocate the technique because it is flexible and easily tailored to a wide variety of field research problems, it addresses explicitly

data derived from counts, and it results in inherently low rates of Type I error.

Although superficially similar to the chi-squared technique (and sometimes used subsequent to it), utilization tests based on the Bonferroni inequality are not familiar to ornithologists. We checked the last 5 yr of issues (1986–1990) from the journals *Auk*, *Condor*, *Wilson Bulletin* and *Journal of Field Ornithology*, encountering only four applications of the technique. The technique could have been, but was not, applied in an additional 85 cases to obtain more informative results. Oversight of this procedure is not unexpected given more widespread use and original introduction in another biological discipline (wildlife science; Neu et al. 1974), without clear indications of the actual computations involved (Byers et al. 1984). Comparative evaluations of the test's performance (Type I and II error) are relatively recent (Alldredge and Ratti 1986), and less-conservative critical regions for some test statistics are still being elaborated (e.g., Hochberg 1988, Rom 1990, Simes 1986). Additionally, utilization tests are not described in most standard statistical textbooks, nor do they typically appear in packages of statistical software.

In this paper, we provide complete information for conducting utilization tests. We first outline the general problem, detail all computations, indicate the types and locations of necessary statistical tables, and examine how test assumptions are satisfied. As examples, we investigate marine habitat preferences of Short-tailed Shearwaters (*Puffinus tenuirostris*) and prey preferences of Crested Auklets (*Aethia cristatella*) in the northwestern Bering Sea, Alaska. We conclude with recommendations for why this technique is favored over more widely-known and -used statistical approaches, particularly those that rely upon numbers of arbitrary observation intervals (such as line transects) rather than numbers of birds as individual sample units.

THE PROBLEM

An investigator often wishes to know whether seabirds exhibit preferences for one or more categories of marine resources. These resources could be physically-differentiated oceanographic habitats (Haney 1989), prey patches (delineated acoustically [Heinemann et al. 1989] or visually [Obst and Hunt 1990]), and prey types classified by species, size or sex (Erikstad and Vader 1989). We formally define "use" as the proportion of the observed seabird study population taking or inhabiting a particular resource. "Selection" implies a much narrower connotation in meaning, i.e., resource use in greater or lesser proportion to actual occurrence/availability in the environment. When data consist of counts, and predictor (independent) variables are categorical, goodness-of-fit statistics such as χ^2 and G are often used (Sokal and Rohlf 1981:691–778). Some goodness-of-fit techniques often give no definitive, statistical indication of whether or not specific resource types are preferred when the categories number three or more (Byers et al. 1984, Neu et al. 1974). Furthermore, if many pair-wise comparisons for each combination of resource categories are

undertaken (e.g., several chi-squared tests), there can be general failure to control for the experiment-wise error rate (α) during the testing procedure unless more sophisticated options are employed (see Agresti 1990).

By setting an upper bound on the overall significance level α , the Bonferroni inequality gives one solution to the predicament of conducting multiple tests of significance (Miller 1981:67-70). This thereby enables an investigator to obtain more specific information regarding the individual resources used or selected by the study animals (Neu et al. 1974).

COMPUTATION

When testing for either resource use or selection, the investigator must first determine expected proportions (p_{io}). If the hypothesis is that bird use is independent of resource categories, and sampling effort across or bird access to all categories is equal, values for the expected proportions will take on the value $1/k$, where k equals the number of categories. If sampling effort across resource categories is not equal, then proportions for expected use will take on values corresponding to relative sampling allocation within each category (e.g., length of line transects within each habitat; Table 1). When measures of resource availability are possible, such as areal assessments of habitat size based on synoptically-mapped environmental data (Haney 1989), then expected values for resource selection can be determined by calculating the relative amounts of each resource type actually available to the birds.

Observed proportions (p_i ; $i = 1$ to k) for determining resource use are obtained from field surveys and censuses (fraction of the seabird study population located within habitat types), or collection, pellets, and regurgitations (fraction of the population taking certain prey types). If the purpose of the investigation is directed only towards making a statement about use of a single, preselected resource type ($i = 1$), a confidence interval on the observed proportion (p) is constructed with the following formula:

$$p - Z_{(\alpha/2)}\sqrt{p(1-p)/n} \leq p \leq p + Z_{(\alpha/2)}\sqrt{p(1-p)/n} \quad (1)$$

where p = the observed proportion, n = the total number of birds observed or collected, and $Z_{\alpha/2}$ = the upper standard normal table value corresponding to a probability tail area of $\alpha/2$. If 0.05 is used as the conventional value for α , Z takes on the value 1.96 (see Table A3 in Snedecor and Cochran 1980:468). With prior knowledge, testing for a single resource type would be mandated if the investigator wants to know only if seabirds are preferentially taking a single size class of prey also targeted by a commercial fishery (cf. Duffy et al. 1987), or whether seabirds are more common within or at a single identified habitat (e.g., water mass discontinuity or ocean front; Brown 1980). In such cases, formula (1) would be used in place of calculating simultaneous confidence limits.

Otherwise, that is if confidence intervals are to be figured on all observed proportions (p_i), the following formula is used for each resource category:

$$p_i - Z_{(\alpha/2k)}\sqrt{p_i(1-p_i)/n} \leq p_i \leq p_i + Z_{(\alpha/2k)}\sqrt{p_i(1-p_i)/n}, \quad (2)$$

where p_i = observed proportion for the i^{th} resource, n = the total number of birds observed or sampled, k = the number of resource categories, and $Z_{(\alpha/2k)}$ = the upper standard normal table value corresponding to a probability tail area of $\alpha/2k$. Confidence limits figured with formula (2) control for the experiment-wise error rate and, for a single resource category, will always be wider than a confidence limit figured with formula (1). When the expected proportion (p_{io}) lies, respectively, either above or below the confidence limits calculated with formulae (1) and (2), one can conclude that seabirds are using any individual resource less than or more than expected by chance.

A short cut for figuring simultaneous confidence limits on sets of observed probabilities is available ($p_i \pm [Z_{(\alpha/2)}]/(2\sqrt{n})$; Fitzpatrick and Scott 1987). It is less accurate, however, than formula (2) or an alternative method of computation based on the χ^2 distribution described by Goodman (1965:247-248).

TEST ASSUMPTIONS

The most critical assumption for this procedure is that resource types must be truly accessible to the seabirds. Type I error can result if prey types or size classes outside the handling abilities of the birds are included (cf. Hulsemann 1981). When testing for resource selection across prey types, and availability has been estimated from trawls, plankton nets or similar gear (e.g., Erikstad and Vader 1989), capture avoidance by the prey can easily result in biased values for expected proportions. Similarly, hydroacoustic surveys of potential prey abundance should use only information integrated from that part of the water column actually accessible to the birds (e.g., within diving depth range). If surface oceanographic habitats are the resource types tested, they too must be equally-accessible to the birds. This is less likely to cause bias given 1) behavioral and morphological abilities of highly-mobile seabirds to move across heterogeneous environments and 2) with respect to this capacity, speeds and time-frames for ship-board sampling are relatively slow and long, respectively. Bias might result, however, if habitats are chosen in such a manner as to be located beyond the commuting ranges of birds foraging from colonies, or if aerial surveys were repeated over the same locations at very short time lags.

Data must be collected so that birds observed repeatedly do not result in correlated samples (Beal and Khamis 1990). Even when birds are censused from moving ships, investigators should take precautions to prevent recording birds that are circling or following (Gould and Forsell 1989:6). When assessing dietary preferences, observations should originate preferably from different locations, and always on different birds rather than from the same individuals resampled at different points in time. If the same areas are repeatedly censused, enough time should elapse to preclude collection of correlated data. For example, if repeated ship-

board surveys are made near colonies, then lags of days or perhaps hours can allow for bird locations to change in response to environmental conditions, or as individuals commute back and forth to colonies. Observations should be collected from a number of different sites or times within each resource type in order to prevent unlucky correspondences between the location of temporary, socially-facilitated groups of seabirds (e.g., Hoffman et al. 1981) and the location of the resource. During assessments of habitat preferences, this bias can be minimized by choosing habitat categories with dimensions larger than spatial scales characteristic of social attraction and interaction.

Sample sizes must be sufficiently large to enable a valid approximation to conditions of binomial experiments. A rule of thumb is to obtain sample sizes (n) large enough such that both $n(p_i)$ and $n(1 - p_i)$ are ≥ 5 , conditions found to be conservative through simulation (Allredge and Ratti 1986). Aside from adherence to conditions of binomial experiments, utilization tests do not require the normal distributions characteristic of most parametric statistics. Type II errors can occur if sample sizes (number of birds) are small, or when the number of resource categories chosen (k) is very large (Allredge and Ratti 1986). Finally, because experiment-wise error rates are controlled in such a way that they are *no greater than* the specified level (e.g., 0.05), utilization tests based on the Bonferroni procedure are quite conservative and may result in very low power.

EXAMPLES OF THE PROCEDURE

We tested for resource use by Short-tailed Shearwaters (habitat) and Crested Auklets (prey) in the northwestern Bering Sea, Alaska. In neither situation could availabilities of the resources be conclusively determined, so we were not able to test for selection. Expected values for occurrences of shearwaters in each of four different oceanographic habitats were calculated based on the relative amount of line transect sampling conducted in these habitats (Table 1). Habitats were characterized by environmental measurements recorded concurrently with seabird surveys. After comparing expected to observed proportions with simultaneous confidence limits (formula [2]) for each of the four habitat categories, we found that shearwaters preferentially used areas characterized by mixed/turbulent water and areas with a shallow (≤ 9 m) pycnocline (Table 1). Shearwaters used areas with a deep pycnocline (9–24 m) less than expected by chance. These findings are biologically pertinent given the following: 1) shearwaters may seek out prey associated with pycnoclines (or thermoclines; see reviews by Brown 1980, Hunt and Schneider 1987) or brought to the surface by mixing (cf. Brown and Gaskin 1988), 2) shearwaters are only capable of shallow dives (Brown et al. 1978), and 3) most foraging by procellariiforms is limited to the upper 10 m of the water column (Jackson 1988).

Several studies have indicated that Crested Auklets take mainly *Thysanoessa* euphausiids in the northern Bering Sea (Bédard 1969, Piatt et al. 1988). Diet items from 46 adult Crested Auklets were used to test the

TABLE 1. Differential use of oceanographic habitats by Short-tailed Shearwaters ($n = 5692$) counted from 745.5 linear km of ship-board transects in the northwestern Bering Sea, Alaska. Transects originated from three different censusing lines (sampled once, twice, and six times, respectively) surveyed on nine different days between 20 August and 1 September 1987. Tests are based on individual comparisons of observed proportions (p_i) to expected proportions (p_{io}).

Oceanographic habitat	Census effort in km; effort ratio (p_{io})	Number; proportion of shearwaters observed (p_i)	Confidence interval on observed proportion of occurrence (p_i) (95% family confidence coefficient) ^c
Vertically-mixed (unstratified)	175.2 (0.235)	2089 (0.367)	$0.351 \leq p_1 \leq 0.383^a$
Shallow pycnocline (1.5–9.0 m)	42.0 (0.056)	523 (0.092)	$0.082 \leq p_2 \leq 0.102^a$
Medium pycnocline (9.1–16.5 m)	321.9 (0.432)	1902 (0.334)	$0.318 \leq p_3 \leq 0.350^b$
Deep pycnocline (16.6–24.0 m)	206.4 (0.277)	1178 (0.207)	$0.194 \leq p_4 \leq 0.220^b$
Total	745.5 (1.000)	5692 (1.000)	

^a Significantly ($P < 0.05$) greater than expected use.

^b Significantly ($P < 0.05$) lower than expected use.

^c $Z_{(\alpha/2k)} = Z_{(0.05/2/4)} = Z_{0.00625}$. Thus, $(0.5 - 0.00625) = 0.49375$. The corresponding Z value is 2.498 (Table A3, Snedecor and Cochran 1980:468). To set upper and lower confidence limits on each p_i , the Z value is used multiplicatively with the expression $\sqrt{p_i(1-p_i)}/n$ (see formula [2]).

hypothesis that auklets used all prey types equally. The expected proportion under the hypothesis of equal use is 0.167 ($1/k$, $k = 6$; Table 2). The observed proportion is 39/46, or 0.848 (Table 2), and $Z_{i(\alpha/2)} = 1.96$. The confidence limits on the observed proportion are thus $0.848 \pm 1.96 \sqrt{0.848(0.152)/46}$, which equals 0.848 ± 0.104 (formula [1]). As 0.167 lies well below the interval 0.744–0.952, we can state confidently that Crested Auklets preferentially preyed upon *Thysanoessa* euphausiids in this case.

TABLE 2. Dominant prey taken by 46 adult Crested Auklets collected on 30 August 1987 off southwestern St. Lawrence Island in the northwestern Bering Sea, Alaska. Stomach contents only are listed; chick meals (gular pouch contents) are not included (cf. Piatt et al. 1988:97).

Prey species	Number of auklets ^a
Unidentified fish spp.	1
<i>Aglanthe digitalis</i> ^b	0
Calanoid copepod spp. ^c	3
<i>Parathemisto</i> spp. ^d	3
<i>Pseudocalanus minutus</i> ^b	0
<i>Thysanoessa</i> spp. ^e	39

^a Number of auklets for which prey type was the sole or numerically dominant species.

^b One individual present in one stomach, but not numerically dominant.

^c *Calanus marshallae* and/or *Neocalanus plumchras*.

^d *Paramethisto libellula* and/or *P. pacifica*.

^e Adult or furcilia of *Thysanoessa* spp.

RECOMMENDATIONS FOR SEABIRD STUDIES

Results from marine surveys are almost always analyzed comparatively by using the number of intervals (line transects, count periods or stations) rather than birds as individual observations (e.g., Briggs et al. 1987:56–58, Haney 1986, Schneider and Duffy 1985). Not only can this practice result in too few degrees of freedom and greater likelihood of Type II error, but the general approach is entirely arbitrary unless sample intervals and sizes are justified by cost efficiency (Bros and Cowell 1987), statistical power (Hanowski et al. 1990, Morrison 1988) or inference space (delineation on the observed treatments or independent variables; Haney and Solow 1992). The procedure presented here can lessen the arbitrary nature of data analysis. Utilization tests do not incorporate measures of variability *per se* (sampling intervals do not directly affect the test's outcome), thereby preventing the spurious results which can arise solely from inter-interval differences inadvertently caused by sampling layout.

The technique is also quite adaptable to logistical problems that frequently arise at sea. If observer fatigue, weather or transiting different resource types unexpectedly alters a count period, incomplete counts can still be used because expected proportions are figured according to the relative amount of total effort expended within the resource sampled. Heavy fog intermittently prevented completion of some of the line transects conducted in the northwestern Bering Sea (Table 1), but expected proportions were adjusted accordingly, thereby retaining all available information. As ocean-going surveys are conducted within highly-variable marine environments, it is virtually impossible to pre-plan survey layouts such that sampling across all treatments or resource categories is equal (Haney and Solow 1992). If sampling intervals are used as the observations, this can lead to unbalanced designs which consequently have lower sensitivity (increased risk of overlooked significance; see Miller 1986). Utilization tests, however, can incorporate directly unbalanced designs during calculations of expected proportions. Providing that observation records are standardized, utilization tests can also be used with any kind of field survey method. Line transects of any length, strip censuses, timed counts of any duration, and station counts are all amenable to the procedure (see also Tasker et al. 1984).

Partly from failure to recognize explicitly the nature of data collected (counts consisting of whole integers), assumptions for many statistical tests used during marine investigations of seabirds have proved difficult to meet (e.g., normal data distributions: Schneider and Duffy 1985). Utilization tests are an appropriate match to the dependent or criterion variables used in marine field studies because they are specifically designed to deal with enumerated or count data. In contrast, linear correlation is a commonly employed test in field investigations, but serious violations in its assumptions often occur. Because of serial dependency in the independent variables chosen (e.g., sea surface temperature), the effectiveness of linear correlation is limited. To circumvent such problems, uti-

lization tests can be applied after continuous variables are converted to contiguous categorical variables via designation of arbitrary class limits (see Sokal and Rohlf 1981:691, and Table 1). Thus, numbers and interval sizes for categories can remain flexible, ultimately chosen by the investigator to address specific research hypotheses of interest. In addition to mutually exclusive attributes such as prey types (Table 2), tests for utilization can be employed to examine trends in seabird use of resources defined by continuous variables. For example, in situations that test for relationships with a contiguous categorical variable such as pycnocline depth (Table 1), the investigator may be able to specify a numerical threshold where resource preferences change abruptly from significant use to significant non-use (Haney 1991).

The utilization test, as described by Neu et al. (1974), is one of several statistical procedures available for determining resource preferences of birds. It is one of few procedures amenable to systematic transects or similar census techniques, however, and the only one not requiring individually-marked individuals (see Alldredge and Ratti 1986:158). Like any statistical procedure, utilization tests have assumptions, and investigators should become familiar with them. As in all field studies, inferences from subsampling should be extended only to the appropriate target population, time period and location. Although we chose to stress applications to ocean-going field studies of habitats and prey preferences of seabirds, utilization tests can be used during any ornithological study in which greater specificity for determining avian affinities for single categorical variables is desired (e.g., individual classes of behavior, nest site characteristics, genetic alleles, etc.).

ACKNOWLEDGMENTS

Data collection in the northwestern Bering Sea was sponsored partially by the Minerals Management Service (MMS), U.S. Department of the Interior (DOI), through an Intra-agency Agreement (No. 14-12-0001-30391) with U.S. Fish and Wildlife Service (USFWS), U.S. DOI, as part of the MMS Alaska Environmental Studies Program. Additional support was provided by the Alaska Fish and Wildlife Research Center and the Alaska Maritime National Wildlife Refuge, USFWS. John Martin, Captain Al Bayer, and the crew of the *M/V Eagle-Tiglat* provided substantial logistical assistance. A. Schauer, G. Lingle, C. Swafford, A.-M. Furman, R. Dwork, S. Hatch and J. Wells assisted at sea. A. Springer, M. Springer and A. Schauer identified the auklet gut contents. The Sivuqaq and Savoonga Native Corporations and town councils of Gambell and Savoonga granted permission to work at St. Lawrence Island. We thank K. G. Beal and K. Yasukawa for suggestions on an earlier version. Additional support was provided by the Pew Charitable Trusts and the Marine Policy Center's program "Changing Global Processes and Ocean Conservation" at Woods Hole Oceanographic Institution. This is WHOI Contribution No. 7683.

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Received 10 Dec. 1990; accepted 30 May 1991.