



Typological thinking and the conservation of subspecies: the case of the San Clemente Island loggerhead shrike

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Abstract. Hybridization with closely related taxa poses a significant threat to endangered subspecies (e.g. outbreeding depression, inbreeding) and confounds efforts to manage and conserve these taxa through a loss of taxonomic identity, in part because of the practical necessity of defining subspecies in a typological manner. We examined nine morphological characters in 167 post-juvenile museum specimens to determine if loggerhead shrikes *Lanius ludovicianus* Linnaeus 1766 on San Clemente Island (off the coast of California) remain diagnosable as *L. l. mearnsi* Ridgway (1903); an island endemic listed as endangered by the United States Fish and Wildlife Service. Four recent shrike specimens from the island were compared to historical specimens using a bivariate scatter plot and a discriminant function (the latter was used to classify recent specimens post hoc). The few recent specimens were not diagnosable as *L. l. mearnsi*,

but instead appear to be intergrades between *L. l. mearnsi* and *L. l. anthonyi* Mearns 1898 (the subspecies endemic to Santa Cruz, Santa Catalina, Santa Rosa and Anacapa islands), and are perhaps closer to pure *anthonyi*. Our data and the species' natural history and distribution suggest that shrikes currently on San Clemente Island are the result of genetic 'swamping' of *mearnsi* by *anthonyi*. Under a necessarily typological definition of a subspecies, it is evident that *mearnsi* is probably no longer diagnosable. However, we conclude that protection of the entire Channel Islands population of the loggerhead shrike would be the best management strategy, as the species has declined drastically throughout the islands.

Key words. Channel Islands, Endangered Species Act, hybridization, *Lanius ludovicianus mearnsi*, loggerhead shrike, San Clemente Island, typology.

INTRODUCTION

One of the great triumphs of the evolutionary synthesis of the 1930s and 1940s was the development of the biological species concept (Dobzhansky, 1937; Mayr, 1940, 1942). This concept, despite its faults and limitations, brought the definition of a species firmly into the evolutionary fold. It considers populations as the fundamental units in question and incorporates the idea of variation within these populations, something that, it was hoped, would forever rid biologists of 'typological thinking' (Mayr, 1969). Thus, instead of classifying

an organism as belonging to a certain species by how well it matched a designated type, the question was to what extent populations of those organisms interbred with other populations — if populations interbred extensively they belonged to the same species. Furthermore, if individuals in each interbreeding population looked sufficiently distinct, and these populations occupied largely distinct geographical ranges, they were classified as subspecies of that species (Mayr, 1942, 1969).

Conservation biologists are saddled with a difficult task when taxonomists and systematists

resort to typology, as in the designation of a subspecies and with the advent of the phylogenetic species concept (Cracraft, 1983). By definition, subspecies are diagnosably distinct populations that freely interbreed with members of adjoining populations; indeed, subspecies 'can and do interbreed as a natural process whenever they are in contact' (O'Brien & Mayr, 1991). Such interbreeding, if on a small enough scale, may have a negligible effect on our ability to diagnose and protect a rare subspecies; yet this interbreeding can pose a major threat to endangered species or subspecies. Hybridization with closely related taxa can lead to outbreeding depression in the rare population (Templeton, 1986) and can seriously threaten taxonomic and genetic integrity of the endangered taxa (Avice & Nelson, 1989; Wayne & Jenks, 1991; cf. Zink & Kale, 1995). If the population of an endangered subspecies is particularly small, even minimal intergradation with other subspecies could drive the endangered form to extinction or greatly hamper conservation efforts (Kiang *et al.*, 1979; Rieseberg *et al.*, 1989). Thus, taxonomic assessments of endangered subspecies are critical to management and conservation (Geist, 1992), for 'a faulty taxonomy may well turn well-intentioned efforts into fiascoes' (Li & Graur, 1991).

We provide such an assessment for the loggerhead shrike *Lanius ludovicianus* Linnaeus 1766, a passerine that has experienced rangewide declines (Cade & Woods, 1997). From seven to 10 subspecies of the loggerhead shrike are currently recognized (American Ornithologists' Union, 1957; Miller *et al.*, 1957; Phillips, 1986). Four subspecies occur in coastal southern California: *mearnsi* Ridgway (1903) and *anthonyi* Mearns 1898 on the Channel Islands, *gambeli* Ridgway 1887 on most of the mainland and *grinnelli* Oberholser 1919 from San Diego County south into northwestern Baja California (Rea in Phillips, 1986). Loggerhead shrikes on San Clemente Island, ± 50 km off San Diego, were described by Robert Ridgway (1903) as *mearnsi*, a subspecies subsequently found to be endemic (Miller, 1931). As a result of direct and indirect human modification of this island during the 20th century, the population declined drastically (Scott & Morrison, 1990) and *mearnsi* was listed as endangered (United States Fish & Wildlife Service, 1977). A captive breeding programme is under way (Azua

& Lieberman, 1995; Kuehler *et al.*, 1995), along with attempts to control feral cats.

L. l. mearnsi was fairly common in the early part of the 20th century (Howell, 1917). No information is available on its population size between 1939 and the mid-1960s. In recent years it persists only in exceedingly small numbers (Hyde, 1980; Jorgensen & Ferguson, 1984; U.S. Fish & Wildlife Service 1984), with an estimated minimum breeding population of only five pairs in 1988 (Scott & Morrison, 1990) and a wild population of only ± 20 birds (Morrison *et al.*, 1995). Because other loggerhead shrike subspecies occur on the adjacent mainland and nearby islands, as well as uncertainties about the duration of low population levels on San Clemente Island, the possibility exists that birds currently on the island are no longer diagnosable as *mearnsi*. Such a situation could result from extinction, with subsequent invasion of the island by another subspecies or from genetic swamping as a result of an extended population bottleneck of *mearnsi* coupled with occasional immigration by one or more individuals from nearby populations. Using morphological analysis, we attempted to ascertain whether the extant population on San Clemente Island is still within the range of variation for *mearnsi* as originally described.

Loss of identity in itself may mean little if the goals of conservation are protection of genetic diversity (Chambers & Bayless, 1983). Even so, a taxon needs to meet a typological 'species' definition to satisfy criteria used in the United States Endangered Species Act and other conservation laws, placing a premier on identity. Furthermore, although all subspecies are not equals, morphological distinction often correlates with genetic diversity, such that any loss of unique characteristics (in this case plumage and morphology) potentially heralds the loss of genes. Determination of which subspecies capture adaptive variation — and are thus evolutionarily significant units (Ryder, 1986; Rojas, 1992) — and which merely capture minor clinal variation is critical, but also time- and cost-prohibitive in many circumstances. To that end, diagnosability, particularly if by multiple characters, may prove to be an important surrogate. The continued identity of distinct subspecies, in this case the San Clemente Island shrike, becomes critical to our efforts to conserve variation within species.

Table 1 Sample sizes of Loggerhead Shrike *Lanius ludovicianus* specimens used to quantify morphological differences between subspecies

Subspecies/locale	Total	Male	Female
<i>L.l. anthonyi</i>	67	40	27
Santa Rosa I.	16	7	9
Santa Cruz I.	23	15	8
Anacapa Is.	2	0	2
Santa Catalina I.	26	18	8
<i>L.l. mearnsi</i>	19	15	4
<i>L.l. gambeli</i>	48	28	20
<i>L.l. grinnelli</i>	29	16	13
Subspecies uncertain	4	1	3

METHODS

Specimen analysis

To develop criteria for classifying current specimens, we examined post-juvenile specimens ($n = 167$) of four subspecies of the loggerhead shrike, *mearnsi*, *anthonyi*, *gambeli* and *grinnelli*, and a small sample of 'sonoriensis' Miller 1930, generally considered synonymous with *excubitorides* Swanson 1832 (Phillips, 1986), from deserts to the east. All specimens were from allopatric populations. Ninety specimens were from the California Channel Islands, including 19 *mearnsi* collected from 1897 through 1939 and four San Clemente birds that died in the captive-breeding programme (Table 1). We were able to examine $\pm 75\%$ of extant specimens of the loggerhead shrike from the Channel Islands (an additional three *mearnsi* and 31 *anthonyi* specimens were unavailable). Specimens were assigned to age and sex class. Ageing was based on rectrix shape (Pyle, 1997), which was at least 90% accurate (based on assessing tail shape with birds of known age).

We examined nine plumage and mensural characters (sexes were combined unless otherwise stated). Eight morphological characters were selected for apparent utility in previous studies (Ridgway, 1906; Miller, 1931; Phillips, 1986). We derived notch-to-tip distance on the bill after initial examination of specimens.

1. Nape and upper back colour were scored from 1 (lightest grey) to 5 (darkest), with sexes scored separately as a preliminary assessment suggested that females may average browner.

2. Feathers between the far lower back (the 'rump' of most authors) and tail were scored from 1 (lightest) to 5 (darkest).
3. Flank colour was scored from 1 (lightest) to 5 (darkest) using the average score from each flank for a given specimen (in two cases only one side could be assessed).
4. The portion of the white stripe above and behind the eye (the superciliary) was scored for contrast and extent from 1 (lightest/most extensive) to 5 (absent or virtually so) and was assessed on both sides and averaged (in two cases only one side could be assessed).
5. Whiteness of the scapulars in contrast to the grey central back and upper wing coverts was judged for contrast and extent, on a scale of 1 (lightest/most extensive) to 5 (absent or virtually so), with scores for each side averaged (in one case only one side could be assessed).
6. The maximum length of white spots on the outermost (lateral) rectrices was measured on both feathers and averaged (in six cases only one side could be assessed — in a few cases this spot was continuous to the base so specimens could not be scored).
7. Bill length from distal edge of nostril to tip was measured on the right side of the bill (a few specimens with broken or damaged bills could not be evaluated).
8. Bill width was measured at the widest point across the centre of the nostrils (a few specimens with damaged bills were not evaluated).
9. Distance from the bill notch to the sharp, hooked bill tip (broken bills and bill tips precluded some measurements). A few characters described above were not checked on specimens of *gambeli* and *grinnelli*.

Individual specimens were reassessed at random to confirm that scoring was consistent; there were no changes in scoring in more than 40 checks among all characters. We performed colour scoring using designated standard specimens in strong, indirect, natural lighting. Not all specimens could be scored on every character as a result of staining, moult and feather or bill damage.

Data analysis

Differences between age classes and between sex classes within each subspecies were determined

Table 2 Selected 75%-rule separations between racial groups (see text for discussion and further information). Sex and age codes are m = male, f = female, d = definitive plumage, 1 = first year, + = d and 1 combined. 'C.O.D.' is the coefficient of difference (Mayr *et al.*, 1953). Two 75%-rules were employed, the first for 75% from 97% and the second for 75% from 99%. A '+' indicates separation exists in both directions, whereas a '1' means separation exists in only one direction. Back colour score was divided by rump colour score for this last test

Character	Subspecies	Sexes	Ages	Sample sizes	C.O.D.	75%-rules	
Back colour	<i>anthonyilgambeli</i>	m	+	33, 24	1.76	++	
		m	d	2, 15	4.77	++	
	<i>mearnsilgambeli</i>	m	1	9, 8	3.28	++	
		f	+	4, 20	2.63	++	
	<i>mearnsilgrinnelli</i>	m	+	14, 15	1.68	+1	
		m	d	2, 8	1.99	11	
		m	1	9, 4	2.24	++	
		f	+	4, 13	2.34	++	
		f	+	4, 13	2.34	++	
Rump colour	<i>anthonyilmearnsi</i>	m	+	34, 14	2.34	++	
		m	1	19, 11	2.61	++	
		f	+	22, 4	1.71	++	
	<i>mearnsilgambeli</i>	m	+	14, 26	1.20	11	
		m	1	11, 9	1.33	11	
	<i>mearnsilgrinnelli</i>	f	+	4, 13	1.49	11	
		f	1	4, 5	2.24	++	
	Flank colour	<i>anthonyilmearnsi</i>	m	+	33, 13	1.33	11
			f	+	19, 4	1.51	11
Back/rump	<i>mearnsilgrinnelli</i>	f	+	12, 13	2.23	++	

with Mann-Whitney *U*-tests. Samples were pooled in subsequent tests when differences between classes were not significant. We tested specimens grouped by *U*-tests to determine the historical validity of taxa (Table 2). The first test was the coefficient of difference (Mayr *et al.*, 1953), defined as the larger mean minus the smaller mean, divided by the sum of the two standard deviations. A result greater than one implies a taxonomically useful difference.

The second and third tests are forms of the '75%-rule', defined as the separation of 75% of each population from 99% of the other (Amadon, 1949). Amadon used sample values to estimate separation for entire populations (parametric values) and did not simply separate specimens at hand (sample values). Variations of this rule include separation for 'all' characters of 84% from 84% (Pimentel, 1958) and separation of 75% from 97% (Mayr, 1969). In his review of all bird subspecies described in the United States from 1957 to 1987, Browning (1990) stated that he used 'the more stringent criterion' of identification of 95% of specimens. However, his criterion is

not directly comparable because he made no distinction between estimating parametric variation and examining a particular collection of specimens and did not make the important distinction between reproducible separations based on data and simply 'choosing correctly' 95% of the time. Museum specialists often can diagnose two populations by subtle criteria difficult or impossible to describe, let alone measure in a reproducible way; we therefore prefer statistical definitions (Amadon, 1949; Mayr, 1969).

We prepared a bivariate scatterplot using combinations of variables that provided good separation of the subspecies. We calculated a discriminant function for the historical samples of *mearnsi* and *anthonyi* to classify recent San Clemente Island specimens. Correct classification using the discriminant functions was examined as the posterior probability of group membership from Mahalanobis D^2 values (BMDP, 1990). Four specimens, three of which were from the current San Clemente Island population, were post hoc classified using these discriminant functions.

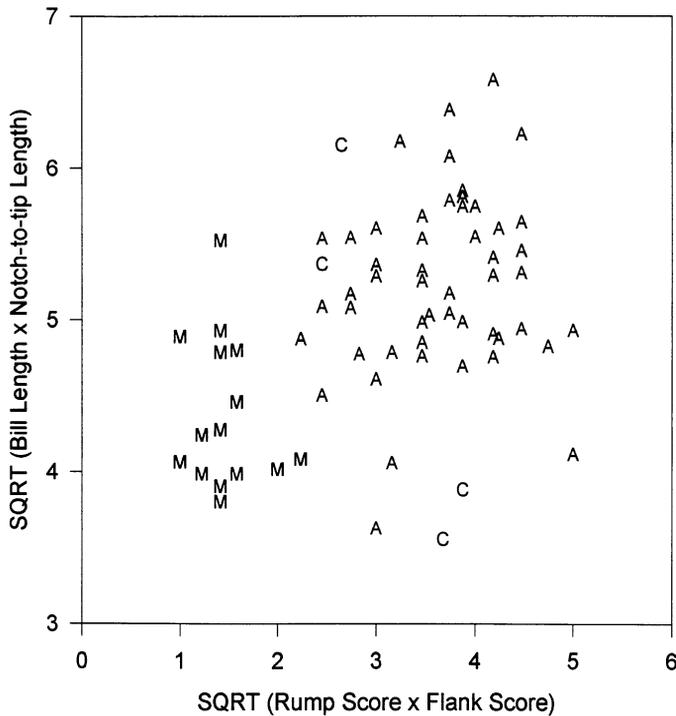


Fig. 2 Bivariate scatterplot of specimens of *L. l. anthonyi* (A), *L. l. mearnsi* (M), and shrikes recently taken San Clemente Island that were post hoc classified (C). Axes are derived values, with those values transformed by taking the square root to increase normality of the samples (Sokal & Rohlf, 1995).

were classified as *mearnsi*. The few specimens of each subspecies falling close to the region of separation on the scatterplot might be genetically intermediate but more likely represent variation within each subspecies.

Our data support *mearnsi* as a valid taxon. Further analysis of variation within both *anthonyi* and *gambeli* is needed to elucidate fully their systematic relationship, although recent molecular evidence supports our conclusion (Mundy *et al.*, 1997). Some Santa Catalina Island *anthonyi* show a degree of intermediacy toward *mearnsi* and some *gambeli* in coastal southern California show intermediacy toward *anthonyi*, perhaps as a result of climate similarity (Miller, 1931). Further study should examine the possibility of differences within *anthonyi* among the Channel Islands, although we saw no indication of this tendency.

We were able to score three of the four recent specimens from San Clemente Island (SDNHM 47803, SDNHM 47822 and SDNHM 48102) on

all four of the characters used in the discriminant functions. Each bird fell closer to the core of *anthonyi* data points than to the core for *mearnsi*, although they had somewhat atypical bill measurements for *anthonyi*. One specimen (SDNHM 47803) has the smallest bill value for any Channel Island shrike, perhaps the result of bill tip breakage, especially likely as it was caged. Caging (which restricts opportunity for bill use) may also explain the measurement for a captive bird whose bill length is well above the mean for *anthonyi* (SDNHM 48102). In any event, two recent specimens were classified as *anthonyi* (SDNHM 47803, $P = 0.96$; SDNHM 48102, $P = 0.93$) and one was classified as a *mearnsi* (SDNHM 47822, $P = 0.96$). Note that all three specimens were classified as intermediates with respect to historical *mearnsi* and *anthonyi* specimens (Fig. 3), suggesting intergradation. Six extant *anthonyi* specimens also fall out as intermediates using that function, supporting the observation by Miller

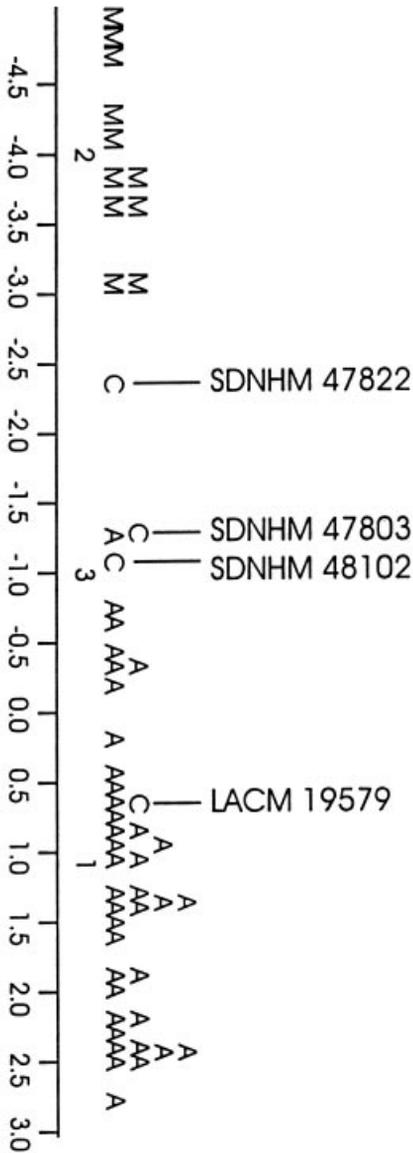


Fig. 3 Histogram from canonical discriminant function analysis of Channel Island shrikes of frequency (the ordinate) of canonical discriminant scores (the abscissa). Note that specimens from San Clemente Island that were post hoc classified (C, mean score denoted by '3') fall between distinct groupings for *L. l. anthonyi* (A, mean score = '1') and *L. l. mearnsi* (M, mean score = '2').

(1931) that *anthonyi* on Santa Catalina Island are intermediate to *anthonyi* on the northern islands (Santa Cruz, Santa Rosa and San Miguel) and to *mearnsi*.

As a result of both small source populations (one of which is now endangered, precluding further collecting) and the need to split samples into sex and age classes (see Collister & Wicklum, 1996), the available sample size of recent specimens may appear problematically small. However, island subspecies with smaller populations tend to be less variable than more widespread, mainland subspecies (Mayr, 1942), although not necessarily equally in all characters (Power, 1983), de-emphasizing the importance of larger current samples. Furthermore, note that our discriminant function is conservative in assuming prior probability of group classification to be 50% for *mearnsi* and 50% for *anthonyi*, rather than weighted for the number of specimens of each. Thus, our function is more likely to classify a specimen as a *mearnsi* than it would if we assumed the prior probability was proportional to the number of *mearnsi* specimens available (in this case 19 of 90, or 21%). Lastly, if we assume that any shrike taken from San Clemente Island should by definition be a *mearnsi* with, conservatively, a 95% probability, then the probability that all three fully scored recent birds would fall out as *anthonyi* or close to it is 0.05^3 or $P < 0.001$. An even more conservative allowance that only 75% of shrikes on San Clemente Island are classifiable as *mearnsi* yields a probability of 0.25^3 or $P < 0.02$ that all three fully scored recent birds would be classified as *anthonyi*.

DISCUSSION

We explored four hypotheses that might explain intermediacy of recent San Clemente Island shrikes relative to historical *mearnsi* and *anthonyi*. First, specimens obtained from the breeding programme may not be representative of the existing population of loggerhead shrikes breeding on the island. All four newer specimens were from the breeding programme and two were siblings (SDNHM 47803 and SDNHM 48102). Two of the four died as yearlings in 1991 and two died in 1992. If all shared the same or similar parentage, their parents could include an *anthonyi*-like or pure *anthonyi* parent, while most birds currently

on San Clemente Island remain pure or nearly pure *mearnsi*. However, 12 free-ranging and captive birds studied closely on San Clemente Island immediately following museum work resembled the four recent specimens (Campbell, personal observation). Additionally, photographs of captive, hand-held shrikes taken on San Clemente Island during Scott & Morrison's (1990) study show *anthonyi*-like characters.

Secondly, perhaps *mearnsi* died out some time between 1939 and the 1980s, before regular monitoring, and was replaced by a population of *anthonyi*. Whereas there is no direct morphological evidence to support or refute this hypothesis, it seems unlikely and molecular data do not support it (Mundy *et al.*, 1997). Campbell observed one bird within the range of variation of *mearnsi*, along with several that appeared to be pure *anthonyi* or intergrades, on the island in 1994. If the current San Clemente Island population represents birds from Santa Catalina Island they would perhaps appear intermediate between *mearnsi* and *anthonyi* (Miller, 1931).

Thirdly, genetic drift in *mearnsi* coupled with a severe population bottleneck could have driven birds to become phenotypically similar to *anthonyi*. Using the harmonic mean (Hartl & Clark, 1989: 83), we estimated effective population size (N_e) of wild *mearnsi* to be only 18 based on 1984–92 census data (Morrison *et al.*, 1995). The population of *mearnsi* was at least this small throughout the 1970s (Scott & Morrison, 1990), so the N_e for *mearnsi* has been fewer than 20 individuals for the past 25 years. With population levels being extremely low for so long, surviving birds could have diverged from earlier representatives as a result of random gene frequency changes in the population's makeup and from inbreeding. Genetic drift suggests that shrikes currently on the island, having recovered only slightly from the bottleneck, would be strongly homogeneous both genotypically and phenotypically (Nei *et al.*, 1975; Carson, 1990). Variation among shrikes currently on the island indicates that this hypothesis is not correct. Furthermore, this hypothesis assumes that the population's morphology drifted by chance in the direction of its nearest neighbouring subspecies (both geographically and systematically), an unlikely random event.

The fourth hypothesis, which we believe best explains the current situation, is extensive intergrada-

tion of *mearnsi* and *anthonyi*. In this scenario occasional immigration of *anthonyi*, of little effect when the population of *mearnsi* was sizeable, began to swamp out characters of *mearnsi* when its population crashed. Immigration can quickly devastate a bottlenecked population of a closely related taxon (Brown & Kodric-Brown, 1977) because 'for any population, a little bit of gene flow goes a long way' (Ellstrand, 1992). Gene flow via immigration can play a crucial role in alleviating inbreeding depression in small, isolated populations of like taxa (Wright, 1931; Shields, 1993). If, however, taxa are unlike but closely related, the taxon with the small population is threatened with extinction via hybridization (Kiang *et al.*, 1979; Cade, 1983; Reiseberg *et al.*, 1989; Ellstrand, 1992). Concomitant with gene flow from *anthonyi*, extensive human modification of the island undoubtedly changed selective regimes. We believe this immigration hypothesis to be the most plausible for explaining morphological similarity to *anthonyi* of shrikes currently on San Clemente Island.

Hypotheses two and four require the ability of loggerhead shrikes to immigrate to San Clemente Island from other populations. The species has wandered to Southeast Farallon Island off the coast of San Francisco (Pyle & Henderson, 1991), those Channel Islands where it does not breed (Garrett & Dunn, 1981; Patten, personal observation), and Islas Los Coronados just south of the Mexican border (Jehl, 1977). It has been observed that 'shrike migration to and from [San Clemente] island is a plausible but currently untested hypothesis. Movement of shrikes across the smaller body of water (35 km) between San Clemente and Santa Catalina islands also should be possible' (Scott & Morrison, 1990). Supporting evidence is also provided by the 1939 *anthonyi* specimen (LACM 19579) and a shrike found dead on the adjacent mainland coast at Coronado in 1996 that was banded and released on San Clemente Island as part of the putative *mearnsi* population (T.A. Campbell, personal communication). It is likely that other subspecies occasionally appear on the island as either migrants (*gambeli*) or dispersants (*anthonyi*, *gambeli* and *grinnelli*). It is also reasonable that they might stay to breed because female loggerhead shrikes show little philopatry, even as adults (Haas & Sloan, 1989; Collister & De Smet, 1997).

Even if this 'swamping' hypothesis is correct, there may yet be diagnosably 'pure' *mearnsi* on San Clemente Island, along with birds representing a wide range of parentages. Recent molecular work detected the presence of a predominant mitochondrial DNA (mtDNA) haplotype in shrikes from San Clemente Island (Mundy *et al.*, 1997). However, their findings do not conflict with ours because the *anthonyi* haplotype, not found in either mainland shrike subspecies examined (*gambeli* and *excubitorides*), was also detected on San Clemente Island. Also, as a result of the maternal transfer of mitochondria in vertebrates (see Cronin, 1993; Avise, 1994), even an F_1 hybrid male *anthonyi* × female *mearnsi* would be indistinguishable from a pure *mearnsi* in terms of its mtDNA. It follows that if recent *anthonyi* immigrants to San Clemente Island have been males, then nuclear genetic swamping may be nearly complete despite distinct mtDNA haplotypes retained in the population.

CONCLUSIONS

Subspecies are *defined* by degree of differentiation and thus are inherently typological. The typological nature of the subspecies limits to what extent evolutionary change or environmentally imposed variation is tolerated before a taxon no longer meets the defined criteria for that subspecies' description. Because subspecies are also defined as not being reproductively isolated from closely related taxa, their conservation is a complex task — a certain level of gene flow must be incorporated into the definition when deciding what to protect. Allowing too little gene flow is problematic because only species would qualify for protection. However, if there is a significant amount of gene flow, particularly if not symmetric between populations, then it might be impossible even to name a subspecies. Attempting to protect populations instead of named taxa is not necessarily a solution, for it is a sad fact that named subspecies are far more likely to be conserved than are unnamed populations (Rojas, 1992). Thus, the careful quantification of subspecific differences, although typological, is of utmost importance in conservation and management efforts (Johnson *et al.*, 1998), however important it may be to conserve distinct populations (cf. Lesica & Allendorf, 1995).

Our morphological analyses indicate that loggerhead shrikes on San Clemente Island are no longer assignable to the *mearnsi* subspecies. Instead, they appear to be hybrids or intergrades between *mearnsi* and *anthonyi*, although the presence of a predominant mtDNA haplotype in San Clemente Island shrikes (Mundy *et al.*, 1997) may yet qualify the population as a distinct evolutionary unit (Rojas, 1992; Moritz, 1995). It is imperative that all shrikes currently occupying San Clemente Island be examined in detail. Bill measurements should be taken and rump and flank colour assessed, either against standard specimens or standard grey-scale cards. Future casualties should be prepared as study skins before the carcass is subjected to necropsy.

We agree that a 'hands-on' management approach should be continued for the preservation of *L. l. mearnsi* (Cade & Woods, 1997). However, following a strictly typological definition of a species, as employed by the federal Endangered Species Act, it may be necessary to breed only shrikes that retain largely pure *mearnsi* traits to the exclusion of birds with distinctly *anthonyi* traits. Whereas a programme of back-crossing may yet save *mearnsi* from extinction (as a diagnosable taxon), similar efforts with the dusky seaside sparrow *Ammodramus maritimus nigrescens* Ridgway 1873 proved fruitless from the perspective of the United States Endangered Species Act (O'Brien & Mayr, 1991). A proposed policy on treatment of 'Intercrosses and Intercross Progeny' (U.S. Fish & Wildlife Service, 1996) may allow greater flexibility. It is intended 'to aid in the recovery of listed species by protecting and conserving intercross progeny, eliminating intercross progeny if their presence interferes with conservation efforts for a listed species, and fostering intercrossing when this would preserve remaining genetic material of a listed species'. Such issues should be addressed in the captive-breeding programme as soon as possible.

An effort should be made to deduce the population biology of shrikes on San Clemente Island before modification by Europeans. No formal attempt has been made to estimate original population size (W.T. Everett, personal communication). A population viability analysis should be performed (Shaffer, 1981; Lehmkuhl, 1984; Soulé, 1987), with an attempt to assess the likelihood that *mearnsi* has always been dependent on

occasional immigration from other subspecies of shrikes for population stability.

Lastly, it is crucial to assess the status of *anthonyi* populations on the northern Channel Islands, as no estimates of total population sizes or trends exist. There is evidence of significant, perhaps critical, declines (P.W. Collins and R. Klinger, personal communication). The best conservation strategy, satisfying managers and taxonomists, would be protection of the entire Channel Islands population of the loggerhead shrike under the United States Endangered Species Act. We believe this action is justified under the Act, sounder than delisting *mearnsi*, and more effective than present efforts to preserve shrikes only on San Clemente Island.

Regardless of eventual protection and management, the fate of the San Clemente Island shrike has broader implications for the whole of conservation biology. The stated goal of this field is preservation of the organismal diversity, with a recent emphasis on genetic diversity (Chambers & Bayless, 1983; Ryder, 1986; Rojas, 1992; Moritz, 1995). However, genetic diversity only goes so far. If such diversity were never manifested in the morphology, our world would be a duller place. Much of what we know about speciation and evolution is based on geographical variation in morphology. The preservation of valid subspecies is tantamount to preservation of geographical variation, the raw material of evolution. In the case of the San Clemente Island shrike we may have already lost much of this variation. Attempts to preserve it, and like variation in all populations, should be at the forefront of efforts to conserve biodiversity.

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