

# A COMPARISON OF LIFE HISTORY PARAMETERS OF FIVE LANIIDAE SPECIES

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**ABSTRACT.**- Of the 30 shrike species, many are declining or have become locally extinct. A literature search revealed that there is little life-history information for most species. In this paper we focus on the similarities and differences in the life-history parameters of the five most studied species - *Lanius excubitor*, *L. collurio*, *L. ludovicianus*, *L. excubitorius*, and *L. collaris*. Each species' life history was examined for dispersion, distribution of resources, mating systems, territoriality, male-male competition, and mate choice. Based on the data available, we formulated predictions regarding life-histories and their correlation with survival strategies and reproduction. IBCE Tech. Publ. 7:92-101, 1998.

Shrikes belong to the large and diverse order of Passeriformes but more closely resemble Falconiformes in their structure and behavior (Cade 1995). There are 30 species of shrikes in three genera - *Corvinella* (2 species, restricted to Africa), *Eurocephalus* (2 species, restricted to Africa), and *Lanius* (26 species, range through Europe, Asia, Africa, and North America) (Sibley and Monroe 1990, Iseemann and Bouchet 1993). Bold and aggressive, shrikes use their strong, hooked bill to kill and feed on insects, reptiles, birds, and mammals (Schon 1994a, Cade 1995). Shrikes have a range of gruesome names such as 'butcher bird' or 'Neuntoter' (hanger of nine) because of their habit of impaling prey on sharp objects, or in the fork of a tree (e.g., Morris 1851-1857, Donovan 1929, Beven and England 1969, Olsson 1985).

Shrikes are found in a variety of habitats from dry, open bushland to forests. They are sit-and-wait predators that also hunt by hovering (Yosef and Grubb 1993, Yosef 1996). Vertebrate prey is killed by bites to the nape that disarticulates the cervical vertebrae (Cade 1967). The sexes are similar in mass and most species are sexually monochromatic. Shrikes are resident, or short- or long-distance migrants. Within a species, one population may be resident, while another may be migrant, depending on the environmental conditions of the surrounding habitat. A shrike's calls are loud and harsh and many species are good mimics. Although Cramp and Perrins (1993) consider shrikes unsociable in that they never clump or allopreen, recent study has shown that "group-meetings" (average

4 individuals) are more frequent just before and after the phase of the annual cycle when birds are in pairs (Schon 1994b, 1995).

Shrikes are a relatively uniform assemblage of species, with most species exhibiting a monogamous mating system (Verner and Willson 1969), except two (*Lanius excubitor*, *L. ludovicianus*) which are sometimes polygynous (e.g., Yosef and Pinshow 1988). Only four species, all from Africa, are known to breed cooperatively (Nichol 1964, Grimes 1976, 1980, Zack and Ligon 1985a, b).

Of the 30 shrike species, many are declining or have become locally extinct (Yosef 1994). A thorough literature search revealed little life-history information for most species (Temple 1995). In this paper we focus on the similarities and differences in the life-history parameters of the five most studied species - Great Grey Shrike (*L. excubitor*), Red-backed Shrike (*L. collurio*), Loggerhead Shrike (*L. ludovicianus*), Gray-backed Fiscal Shrike (*L. excubitorius*), and Common Fiscal Shrike (*L. collaris*). Each species' life history is examined with special emphasis on dispersion, distribution of resources, mating systems, territoriality, male-male competition, and mate choice. Based on the data available, predictions regarding the relationships between the environment and the species were formulated.

## METHODS

Data were gathered on the above mentioned species from published and unpublished studies. Because of the major gaps in knowledge of the life-history

Fig. 1. Breeding habitat of shrikes.

Northern I	Red-backed I	Loggerhead I	Common Fiscal I	Grey-backed I
I	I	I	I	I
Generalized habitat			Restricted habitat	

parameters, we used the **comparative method** to examine the five most commonly-studied species in this genus. We hypothesized predictions regarding life-histories and their correlation with survival strategies and reproduction. We formulated that: 1) shrikes should respond to low prey availability by changing their diet to include more available prey taxa and should compensate for unpredictable food supplies by incorporating changes in their daily activity; further, migratory shrikes will change their behavior according to resources available in their wintering or breeding grounds; 2) young shrikes disperse after fledging and do not return to the natal area; 3) shrikes must acquire territories capable of supporting adequate prey populations; 4) shrikes use food caches for a number of different purposes; 5) in principle, shrikes will be monogamous because of limited food supplies, and such that both parents will care for the young; and 6) declines in shrike populations are due to decreased reproductive success and subsequent recruitment.

## RESULTS AND DISCUSSION

*The species.*- The species chosen for this study are relatively similar in their habitat choice, mortality rates, food preference, hunting strategies (Table 1) and reproductive parameters (Table 2). As a group, shrikes tend to live in open countryside, using trees and utility poles and wires as perches (Hands et al. 1989, Atkinson 1993, Yosef and Grubb 1994; Table 3, Fig. 1). Their predators are other birds and ground dwelling predators (Yosef 1996). Nests are built in thorny or otherwise generally inaccessible bushes. Most nest losses occur during egg-laying and incubation due to predators, rainfall, flooding, and observer disturbance (e.g., Kuzniak 1991, Diehl 1995, Yosef 1996).

Three of the shrike species considered are migrants (Table 3, Fig. 2). Loggerhead Shrikes are permanent

Parameter	<i>excubitor</i>	<i>ludovicianus</i>	<i>collaris</i>	<i>excubitorius</i>	<i>collurio</i>
Environment	unpredictable	unpredictable	available, low quality	restricted, high quality	Ecotones
Adult mass (g)	50-70	50		m = 55 f = 52	m = 29 f = 32
hunting succes (%)	69-81				
max. lifespan	5y 9mo				7y 5mo
mortality (%)	27-45	53	61	33	
sex ratio	m > f			m > f	1:1
major food	vertebrates	invertebrates	invertebrates	invertebrates	invertebrates
hunting strategy	sit-&-wait	sit-&-wait hovering	sit-&-wait	sit-&-wait	sit-&-wait
impaling	yes	yes	yes	yes	yes
caches	yes	yes	yes	yes	yes

Table 1. Life history parameters of the five shrike species - *Lanius excubitor*, *L. collurio*, *L. ludovicianus*, *L. excubitorius*, and *L. collaris*.

residents in warm, mild regions, but northern individuals migrate south in winter (Yosef 1996). In homing experiments, Red-backed Shrikes traveled between 223-745 miles back to their nesting areas during the breeding season (Matthews 1968).

**Responses to habitat conditions and food supplies.-**

Regardless of use of an area for breeding or wintering, the habitat selected must provide an adequate prey base, roosting habitat, and escape cover (Atkinson 1993). Loggerhead Shrikes in Florida prefer the short grass areas found in grazed pastures. Tall grasses forced birds to hover, a more time-consuming and energetically expensive form of hunting (Yosef and Grubb 1993). However, if the grass is too short, most prey species may be absent (Prescott and Collister 1993). In addition, the presence of predators (e.g. Little Owls, *Athene noctua*) inhibit the frequency of shrike forays and illustrate the vulnerability of juvenile shrikes to predation (Yosef 1993).

Choice of hunting grounds also varied with species

and area. Red-backed Shrike densities are highest in forest-steppe habitats, and lowest in human-impacted landscapes (Kuzniak 1991, Guerrieri et al. 1995). Northern Shrikes also hunted little in agricultural landscapes due to limited perches, little escape cover, and lower densities of prey (Atkinson 1993).

Winter habitats often provide more challenges to successful hunting. Although insects may be more active in short grass areas during cooler weather (Yosef et al. 1993), in northern regions, insects may not survive in snow and low temperatures. Where snow was present, Northern Shrikes left their traditional open areas and concentrated their hunting in riparian areas and forested corridors (Atkinson 1993)(Table 3). These habitats also provide roost sites and protection from wind, which reduces heat loss. Linear habitats (e.g., rimrocks) also become important since they contain crevices for nesting deermice (*Peromyscus* spp.), allowing them to reproduce year round, and providing shelter and warmth for a wide

Parameter	<i>excubitor</i>	<i>ludovicianus</i>	<i>collaris</i>	<i>excubitorius</i>	<i>collurio</i>
First breed	1-2y				
nesting	solitary clumped?	solitary			1-2y clumped
nest height (m)	0.95	0.5-3.0		1-10	
incubation (days)	15-17	16-17		13-15	1-10 0.8-2.4
clutch size	4-7	2-6		3-4	13-15 14
young fledge (days)	15-19	15-17		20	c3-4 3-5
young independent	60				20 22-26
hatching success (%)		81		91	37
fledging success (%)	89	60	15	15	91 95
nestling survival (%)		64			15 87
post-fledging juvenile mortality rate	45	54			
breeding season	Feb-May	Feb-June			40
Region	Holarctic	North America	East and Central Africa	East Africa	May-Aug EurAsia

Table 2. Reproductive success of *Lanius excubitor*, *L. collurio*, *L. ludovicianus*, *L. excubitorius*, and *L. collaris*.

Northern I	Red-backed I	Loggerhead I	Common Fiscal I	Grey-backed I
I	I	I	I	I
LRM	LRM	LRM SRM	Sedentary	Sedentary

Fig. 2. Migratory status of shrikes. LRM denotes long-range migrant, and SRM short-range migrant.

range of potential prey of the shrikes (Atkinson 1993). In Sweden, in winter they hunt mostly vertebrates because of the scarcity of invertebrates (Olsson 1985). Conversely, Loggerhead Shrikes most commonly hunted near pastures, hedgerows, and pasture-hay meadows, but their numbers decreased in harvested cropland and in woodland (Hands et al. 1989, Smith and Kruse 1992). Loggerhead Shrikes in Canada and Florida preferred short grass with some shrubs in pastures for breeding, perches, escape cover, and wintering grounds (Telfer 1992, Yosef 1992a). During the breeding season, suitable habitat for resident Loggerhead Shrikes in South Carolina consisted of a patchwork of short disturbed grasslands and sparsely vegetated cropland, but during the non-breeding season, they increased their relative use of cropland (Gawlik and Bildstein 1993).

A shrike's diet can provide important information on foraging ecology, winter territoriality, resource partitioning, and population regulation (Atkinson and Cade 1993). Shrikes show definite seasonal food preferences, eating primarily arthropods during warmer months, supplemented occasionally with small vertebrates. The annual diet of Loggerhead Shrikes generally comprises 68% insects, 4% spiders, and 28% vertebrates (Bent 1950) and in eastern and western U.S., insects 68 and 83%, spiders 4 and 2%, vertebrates 28 and 12%, respectively (Beal and McAtee 1912). During winter, however, vertebrate prey may constitute up to 76%; small mammals up to 3-55% depending on season and location (Graber et al. 1973, Kridelbaugh 1982, Olsson 1985, Atkinson and Cade 1993).

Northern Shrikes, by comparison, feed more on

Parameter	<i>excubitor</i>	<i>ludovicianus</i>	<i>collaris</i>	<i>excubitorius</i>	<i>collurio</i>
nonbreeding	variable	warm	tropical	tropical	temperate
not migratory	X	X	X	X	
short distance	X	X			
long distance	X	X			X
range contraction	significant	significant	?	?	significant
mating system	monogamy	monogamy	monogamy	cooperative	monogamy
helpers	no	no	no	yes 2-11	no
territory size (ha)	20-215	0.2-14.6		0.5-3.4	0.5-3.4
site fidelity - females	no	no	no	yes	no
males	yes	yes			yes
male feeds female	yes	yes	yes	yes	yes
males feeds young	yes	yes	yes	yes	no

Table 3. Habitat and pair-bond parameters of *Lanius excubitor*, *L. collurio*, *L. ludovicianus*, *L. excubitorius*, and *L. collaris*.

Fig. 3. Mating systems of shrikes.

Common Fiscal Red-backed		Loggerhead Northern		Grey-backed
I	I	I	I	I
I	I	I	I	I
Monogamy		Monogamy with occasional polygyny		Cooperative

vertebrates (Cade 1962, 1967, Atkinson and Cade 1993). However, in Egypt's western desert, Northern Shrikes preyed upon arthropods in direct relation to their availability, rarely taking vertebrates (Hegazi 1981).

The two species also eat roadkills and carrion (Yosef 1996). Red-backed Shrikes in Germany consumed 51% beetles and smaller prey (e.g., ants) were caught only when they occurred in large amounts (Wagner 1993). Hence, shrikes that live in unpredictable habitats should increase their diet breadth by including less acceptable foods of low value, i.e., in winter shrikes should increase the number of suitable prey taxa in their diet to the low overall prey availability. With abundant resources shrikes should narrow their use of prey types and their diet breadth should decrease. The results support this prediction since shrikes are known to have definite seasonal food preferences (see above). This is further substantiated by the fact that during the breeding season, male Northern Shrikes gathered more than 4.83 times the energy they needed, feeding the remainder to their mates and nestlings (Degen et al. 1992).

Dispersal.- After fledging, young shrikes dispersed and did not return to their natal areas to nest (Table 3). However, among adults, dispersal was not equal between the sexes.

Male Red-backed Shrikes exhibit greater site fidelity than females (Massa et al. 1993). In Israel, only male Northern Shrikes exhibit site fidelity (Yosef 1992b). The same appears to be true for Loggerhead Shrikes (Haas and Sloane 1989). In both species there was desertion and mate switching by females (Haas and Sloane 1989, Yosef 1992b).

Haas and Sloane (1989) found that female Loggerhead Shrikes are not faithful to a territory within a breeding season and suggest that desertion

Table 4. Comparison between cooperative and monogamous mating and breeding systems (Zack and Ligon 1985 a, b).

Parameter	Cooperative	Monogamous
example	<i>L. excubitorius</i>	<i>L. collaris</i>
<b>HABITAT</b>		
shrub/tree cover	high	low
temporally stable	yes	no
spatially restricted	yes	no
distributional pattern	accacia woodlands	bradly distributed
insect prey	more	less
disappearance rate	low	high
turnover rate	low	high
<b>TERRITORY</b>		
stability	high	low
type	exclusive	exclusive
<b>YOUNG PER</b>		
pair	less	more
group	more	less
adult	less	more
fledged/successful nest	more	less
juvenile dispersal	low	high
survival	67%	39%
nest predation	high	high

prey taxa in their diet to the low overall prey availability. With abundant resources shrikes should narrow their use of prey types and their diet breadth should decrease. The results support this prediction since shrikes are known to have definite seasonal food preferences (see above). This is further substantiated by the fact that during the breeding season, male Northern Shrikes gathered more than 4.83 times the energy they needed, feeding the remainder to their mates and nestlings (Degen et al. 1992).

and mate-switching by females may contribute to low return rates. Return rate in North Dakota was 28% (8/29) for males and 5% (2/38) for females, and in Missouri 47% (7/15) for males and no (0/15) females returned (Kridelbaugh 1983).

Zack and Ligon (1985a, b) compared dispersal between Common Fiscal Shrikes (habitat generalists) and Gray-backed Fiscal Shrikes (habitat restricted). They showed that in the former species the fledglings disperse great distances. However, if no territory is available, the juvenile of the latter remain in the natal area and wait for an opening which will permit reproduction.

For banded Loggerhead Shrikes, average distance moved between banding and recapture (at subsequent year's territory) was 2.1 km for adult males (4), 1.8 km for adult females (7) (Collister 1994). Collister further observed that although his study area was filled with shrikes in both 1992 and 1993, about 60% of the breeding adults in 1993 were neither study-area adults nor birds hatched on the study area in 1992. DeSmet (1993) concurs with these findings and reported that over half of the 1992 banded adults were replaced by different adults on the same territory during 1993. In southern Idaho 30% (6/20) of banded adults returned the following year, all to their prior territories (Woods 1994). In North Dakota, during 1985-1988, only 14% (10/69) of adults banded were resighted (Haas and Sloane 1989).

This allows us to infer that the cost-benefit ratio for dispersing vs remaining depends on the habitat specificity of the species (Fig. 1, 3). In a widely distributed species, the benefits of dispersing could include the increased probabilities of attaining breeding status and to avoid inbreeding. However, they also face the costs of uncertainty, competition to establish a territory, and increased mortality due to increased exposure to predators. In habitat restricted species, dispersing individuals could gain by remaining in the natal territory where they gain experience, and in the future may obtain breeding

status. Costs to remaining center around intraflock competition (Zack and Ligon 1985a, b).

*Male-male competition and territoriality.*- Males establish exclusive territories that contain a mixture of habitat types (Atkinson 1993)(Table 3). These territories differ in size between species and the resources they contain. In Northern Shrikes, winter territories on the less productive grasslands of North America are larger than winter territories in Europe (Atkinson 1993).

In Israel, Northern Shrike males reside in territories year round and are resource dependent; territories with more perches are smaller (Yosef 1993). Females, however, are not permanent residents and leave immediately after their last broods fledge (Degen et al. 1992). Territory size in Loggerhead Shrikes also decreased with increased density of introduced perches, and increased when perches were removed (Yosef and Grubb 1992).

Male Red-backed Shrikes establish territories where they compete for a mate, feed her during the courtship and incubation, and help in feeding the nestlings (Ricossa and Massa 1988). They occupy a common home range, that may overlap with neighbors, but with an exclusive core area. The degree of overlap changes through the season - minimal during egg laying, to a greater degree after the eggs hatch, and is maximum after the young fledge (Fornasari et al. 1994).

It is assumed that the best habitats are taken first, and late arrivals take marginal habitats. However, since competition for resources is often intense, resulting in decreased time and efficiency of foraging, a territory cannot be too large or the shrike will spend most of its time protecting it to the detriment of his health (Yosef and Grubb 1992). Territory sizes, then, should be a balance between maximizing the resources needed for successful reproduction and minimizing the costs associated with defending these resources. As a result, territory sizes are a function of competition, resources available, and the shrike's functional ability. For example, Northern Shrike territories in Idaho range from 55-357ha (Atkinson 1993). Based on Zack (1986), and Zack and Ligon (1985a, b), it appears that in areas where the species is habitat restricted, and all suitable territories are occupied, cooperative breeding systems evolved.

*Caches.*- Commonly applied terms 'cache' or 'larder' convey notion that impaling is means of food storage (Watson 1910). It is assumed that impaling evolved as feeding adaptation because it enables shrikes to immobilize larger prey than they could otherwise

handle (Smith 1972), or during breeding season when energy demands are high and caching is a way of dividing labor between sexes (Applegate 1977). Reid and Fulbright (1981) suggest that caching may function as mate attraction and once found 23 round-tailed horned lizards (*Phrynosoma modestum*), bird bills, and feathers festooned on torrey yuccas (*Yucca torreyi*) in the territory of a Loggerhead Shrike.

Impaled prey in Loggerhead Shrikes are most frequently observed during breeding season, but can be observed throughout the year (Burton 1990). In Northern Shrikes, cache size peaks just prior to mating and males with larger caches mate earlier and rear more offspring than males with smaller caches. Cache-deprived males failed to breed (Yosef and Pinshow 1989).

Loggerhead Shrikes impale chemically noxious prey (e.g., lubber grasshoppers, *Romalea guttata*) for periods up to 3 d, consuming them afterward, presumably after the poisons have degraded (Yosef and Whitman 1992). During feeding trials, shrikes ate the pyrrolizidine alkaloid protected moth (*Utetheisa ornatrix*) readily but ignored the cantharidin protected beetle, *Lytta polita* (Yosef et al. 1996). Whether the avoidance was a reflection of innate aversion, or of discrimination based on direct experience with the beetles, remains unknown. Thus, while impaling behavior probably evolved to handle prey, over time it came to serve other functions, allowing shrikes to store food, and degrade toxins, or broadcast their appeal as potential mates (Yosef and Whitman 1992).

**Mating systems.**- Avian reproductive success is limited by the amount of food available for feeding young. Most shrike species exhibit a monogamous mating system (Table 3, Fig. 3). However, there appear to be exceptions to the rule. Although Red-backed Shrike appear to be monogamous, extra-pair copulation was proved with the use of modern techniques wherein a neighboring male fathered three of the four nestlings in a brood (Fornasari et al. 1994). Common Fiscals are also monogamous (Zack and Ligon 1985a). Polygyny was also reported in Northern Shrikes in Israel (Yosef and Pinshow 1988) where polygynous males fathered twice as many eggs, spent more time seeking prey than monogamous males, and spent more time exposed to predators while hunting (Yosef et al. 1991). Only the Gray-backed Fiscal Shrikes exhibit a cooperative breeding strategy. They maintain a strict monogamous system wherein there is only one breeding pair per territory, but incorporate helpers of both sexes (Zack 1986).

The Gray-backed Fiscal Shrike and the Common Fiscal Shrike, sympatric in Africa, provide a good comparative example of the different mating systems (Zack and Ligon 1985a)(Table 4). Cooperative breeding systems evolve in areas of high habitat stability, where the habitat is saturated, and with high adult survival (Fig. 3). In such an area, the options available to nonbreeding adults include delayed breeding within the natal territory, dispersal to another territory, floating, and nest or mate sharing (Zack and Ligon 1985a). Brown (1987) suggested that a species could adapt a communal breeding strategy only if they are nonmigratory, and particularly if they protect group-territories. In the present analysis, only the Gray-backed Fiscal Shrike fits the criteria. In the cooperative mating system incubation and brooding are conducted solely by the female and the breeding male supplies her the most food. Comparing within the same species showed that the cooperative breeders with larger groups fledged more young, brought more prey to the nest, and increased fecundity than monogamous pairs. Benefits to helpers include indirect genetic profit, increased survival, and chances for later reproduction. Male helpers eventually acquire breeding status within the natal area, but females have to disperse (Zack 1986). Cooperative breeding occurs in habitats with increased shrub cover that provided increased perch sites and escape cover (Zack and Ligon 1985b).

Since habitat saturation is a critical factor favoring the evolution of cooperative breeding systems (Selander 1964), such a system is not expected to evolve in the shrikes of North America or Europe since breeding habitat is not saturated (Brooks and Temple 1990, Temple 1995) and territories are available for dispersing young. Indeed, socializing of young, a prerequisite for cooperative breeders, does not occur in these areas since the young disperse soon after fledging (Zack 1986).

**Species declines.**- Several long-term studies have documented drastic worldwide shrike declines. Most central European countries have lost over 50% of their breeding populations within the last 15 years (Rothhaupt 1995). The Northern Shrike is extinct in Switzerland, and has almost disappeared from France, Sweden, and Poland (Yosef 1994). The Red-backed Shrike was recognized as extinct in the U.K. in 1989 (Graham 1993). Once relatively common in North America, the Loggerhead Shrike shows alarming declines in many areas (Erdman 1970, Bystrak 1983, Yosef et al. 1993).

Declines have been attributed to avian predators, extensive human influences, drought (Yosef 1994), and mortality on migration or on the wintering grounds (Cade 1995, Temple 1995, Haas and Ogawa 1995).

However, shrikes appear to be suffering on their breeding grounds also because few populations reach the carrying capacity of their breeding ranges (Brooks and Temple 1990).

Shrikes are either patchily distributed within large tracts of apparently suitable habitat, or thinly dispersed over the available habitat. This suggests that environmental variables associated with nesting habitats are not limiting.

In fact, Loggerhead and Northern shrikes often fledge six or seven young/brood and are known to be double and triple brooded in at least part of their range (Yosef and Pinshow 1988, Yosef 1996). The remaining alternatives are high mortality rates on migration (e.g., hunting) or on wintering grounds (e.g., pesticides, predation, competition for prey or suitable wintering habitat; Lynn and Temple 1991). The major factor, however, may be anthropogenic land-use changes.

The greatest concentrations of wintering Loggerhead Shrikes in North America are found in the Gulf coast states (Texas, Louisiana, Mississippi, Alabama). Recent land-use changes in these states involve conversion of pastureland and hayfield to rowcrops, horse and cattle grazing, and removal of shrubs and shelterbelts (Hands et al. 1989, Brooks and Temple 1990, Lynn and Temple 1991). In Sweden, reduction of pastures and planting with conifers has changed the vegetation and insect populations, causing decreases in Red-backed Shrike Populations (Olsson 1995). Throughout Europe, sweeping landscape modifications have prevented populations of Northern Shrikes from rebounding after severe winters (Bassin 1995).

Exceptions to these are those East European countries (e.g., Poland, Hungary, Belarus) where severe economic problems force farmers to resort to traditional farming practices, and to use less pesticides and mechanization, thus resulting in stable or increased numbers of shrikes.

Migrant species may suffer greater levels of mortality since they must compete with resident territorial shrikes who most probably occupy the best areas forcing the migrants to occupy marginal habitats, reducing survival rates (Brooks and Temple 1990). While on migration, shrikes also appear to be hunted out of proportion of their population level in relation to other passerine species by natural predators (Cade 1995) and humans (Severinghaus 1972).

## CONCLUSIONS AND RECOMMENDATIONS

The data support the first seven predictions. However, although most shrikes exhibit a monogamous mating system (prediction 8), ecological conditions may modify the system resulting in the evolution of a cooperative breeding system. Prediction 9 was not supported, which suggests that declines in shrike populations are not due to decreased reproductive success, but due to more complex interactions involving migratory status, resource competition, and dispersal.

We suggest that future studies concentrate on the migratory species emphasizing the routes taken, staging areas, wintering grounds, and any other parameters that may influence survival away from breeding areas. In addition, most other shrike species are not studied and an effort should be made to collect data for most of the species comprising the True Shrikes, such that a more encompassing strategy for the survival of these birds may be formulated and adopted.

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