

COMPETITIVE RELATIONSHIPS OF THE COMMON AND LESSER NIGHTHAWKS

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The study of competition and the resulting inferences, of necessity, have been often indirect. This is because the processes of competition, as currently understood, are often quite ephemeral and subtle. On a basis of species interactions, there are three general situations for which competition often has been invoked as an explanation (Miller 1967): (1) the narrowing of a niche in sympatry (Lack 1944); (2) contiguous allopatry in the absence of an environmental discontinuity (Miller 1964); and (3) character displacement (Brown and Wilson 1956; Hutchinson 1957; Mayr 1963). If these situations do indeed develop as a result of competition, then under certain circumstances their maintenance could require continuing competitive interactions. Thus such situations should provide the opportunity to study competition as a dynamic and vital process. Recent examples of studies performed under these conditions include Willis (1966), Brown (1971), Heller (1971), and Sheppard (1971).

The distribution (fig. 1) and habitat relationships of the Common Nighthawk (*Chordeiles minor*) and the Lesser Nighthawk (*C. acutipennis*) are favorable for the study of factors involved with the competitive interactions of ecologically similar species. The two species are very similar in size, appearance, and general habits. The allopatric ranges of both species include habitats similar to those within the sympatric region. This combination provides a means of evaluating the impact of sympatry on the breadth of habitat utilization of both species. In addition, at several localities within the sympatric distribution, the habitat isolation breaks down, providing the means to study directly the competitive interactions between these species.

STUDY AREAS AND METHODS

Field work was conducted during the breeding seasons of 1968, 1969, and 1970. Specimens for stomach content analysis were collected in 1970. These were obtained from a site in southern New Mexico referred

to as Taylor Well. It is located 17 miles N and 6 miles E of Las Cruces, Dona Ana Co., New Mexico. Taylor Well is in a broad basin running north and south between the San Andres Mountains on the east and the Dona Ana Mountains and the Rio Grande valley on the west. At Taylor Well, which is 6 miles W of the San Andres Mountains, the basin is about 20 miles wide. At the well are a windmill, a corral, and a small pond. Both species of nighthawks often drink at this pond at dusk, and nearly all collecting was done in the immediate vicinity.

The vegetation in this area is typical desert scrub. *Larrea divaricata* is the most conspicuous species, with *Prosopis juliflora* present in fewer numbers. *Baccharis glutinosa* lines the north and south edges of the pond. The elevation at Taylor Well is 4450 ft. East of the well the elevation gradually increases until, at the actual base of the mountains, the elevation is 5200 ft. The San Andres Mountains are comparatively small and generally dry, thus the foothills support desert scrub vegetation for a considerable distance into the mass itself.

C. acutipennis is abundant over all of the Jornada, and penetrates at least as high as 5200 ft in the foothills of the San Andres Mountains. *C. minor* breeds commonly in the San Andres, but it does not seem to utilize the basin for breeding except for those portions adjacent to the mountains. The lowest elevation at which *C. minor* was observed in territorial display was 4 miles E of Taylor Well at 4800 ft.

The time of collection was noted for each of the 155 specimens collected for stomach content analysis. The intact birds were quick-frozen in air-tight plastic bags at -65°C for subsequent weighing and stomach excision. These specimens were in the freezer from 12 hr to 3 days. The stomach contents were preserved in vials of FAA (formalin, acetic acid, alcohol) for later analysis. The empty stomachs were placed with the birds for a second weighing in order to determine weights of stomach contents. The insects were separated, identified, and counted, before being placed in a drying oven at 70°C for 48 hr. Samples were then weighed.

Material for morphological determinations came from the series of specimens collected for stomach content analysis. Skeletal material is now deposited in the collection of the American Museum of Natural History. Methods used for each morphological determination are described in their respective sections.

HABITAT UTILIZATION

Distributional relationships (A.O.U. 1957; Friedmann et al. 1950; Meyer de Schauensee 1966) and habitat descriptions (Selander 1954; Phillips et al. 1964) of the Common and Lesser Nighthawks suggested the possibility

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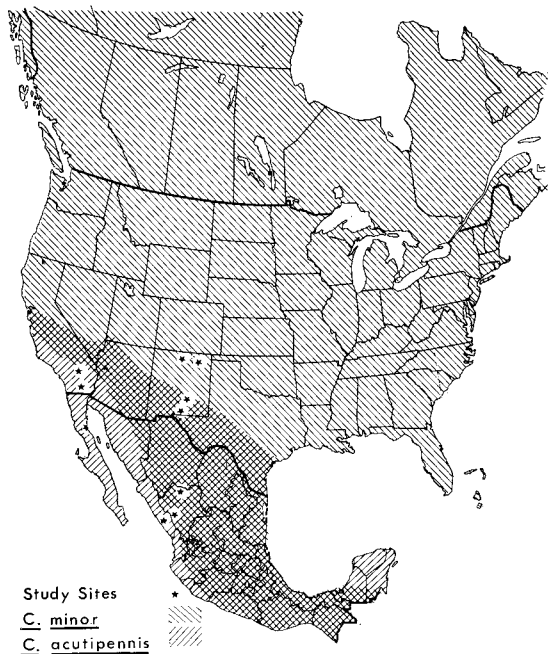


FIGURE 1. North American distributions of *C. minor* and *C. acutipennis*.

that there were differences in habitat utilization between the sympatric and allopatric distributions. It appeared that the breadth of habitat utilization was probably narrower for *C. minor* within the sympatric range. This relationship suggested a narrowing of the niche in sympatry, effected through displacement of *C. minor* from certain habitats by *C. acutipennis*. In order to verify this and to determine the type and direction of the displacement, field work was conducted in each of the allopatric distributions and the sympatric distribution.

HABITAT DISTRIBUTION

Allopatry. The broad geographical range of *C. minor* over most of North America includes a wide variety of habitats from the tropical forests of Panamá (Eisenmann 1963) to the boreal forests of Alaska (Murie 1925).

Field work in the allopatric distribution of *C. minor* was necessary mainly to establish the range of habitat utilization in areas similar to those from which this species is absent in the sympatric range. Much of the vegetation at lower elevations in the southwestern portions of the allopatric distribution of *C. minor* is either short grass prairie or various elements of the sagebrush desert. These vegetation types are either adjacent to or intermingle with the Chihuahuan and Sonoran Desert scrub types which predominate to the south.

Thus there is much similarity in habitats between the southern margin of the allopatric range and much of the sympatric range. Desert scrub was of prime interest within the allopatric range of *C. minor* since this species is generally absent from this vegetation type within the sympatric range.

Field observations were made and specimens collected at a series of localities (fig. 1) in the southwestern portion of the allopatric distribution at various times during the 1969 and 1970 breeding seasons. The vegetation at all the localities was either short grassland, desert scrub, desert grassland, or some intermediate type. Field observations were made in the vicinity of Roswell, Carrizozo, Socorro, Espanola, and Tres Piedras, New Mexico. *C. minor* was found breeding at all of these localities. In addition, Bailey (1928) gives evidence of *C. minor* breeding in desert habitats near Roswell, New Mexico. These observations indicate that in the allopatric range of the southwestern United States, *C. minor* regularly utilizes the arid lowland desert scrub and desert grassland habitats.

Reports by Grinnell (1914), Miller (1951), and Miller and Stebbins (1964) suggest that *C. acutipennis* is limited to desert habitats within its allopatric distribution. On the other hand, several authors indicate that *C. acutipennis* may regularly occur at elevations above those typical of desert habitats. Grinnell and Swarth (1913) reported what might have been a *C. acutipennis* at 4500 ft in the San Jacinto Mountains of California; Grinnell (1928) reported *C. acutipennis* at 6000 ft along the west slope of the Sierra San Pedro Mártir of Baja California; and Anthony (1893-94, 1895) recorded the species from the lower valleys west of the Sierra San Pedro Mártir to as high as 7200 ft at La Grulla, Baja California.

In order to clarify the limits of habitat utilization for *C. acutipennis* within its allopatric range, field work was conducted at three localities 15 June-2 July 1969. The three study areas included portions of the San Jacinto and Laguna mountains of southern California and the Sierra San Pedro Mártir of Baja California.

All three ranges are very steep on the east face, rising abruptly from the lowlands. The inclines on the west are considerably more gentle. The general vegetational aspects in and adjacent to all three mountain ranges are very similar. East of the three mountain ranges the vegetation of the lowlands below 3500 ft is typical desert scrub. *Larrea divari-*

cata, *Franseria dumosa*, and *Dalea californica* comprise the dominant plant species. Above this, on the lower slopes and ridges, chaparral predominates with *Adenostoma fasciculatum*, *Rhamnus californica*, and *Heteromeles arbutifolia* among the more common shrubs. From 5000 ft to about 7500 ft there are varying amounts of pinon-juniper woodland (*Pinus monophylla*, *Juniperus californica*) and/or pine-oak forest. At higher elevations these are replaced by true coniferous forests. Within this last vegetation type, large open meadows are common.

Systematic field observations were made successively in each of the vegetation zones, beginning at the lower elevations, until either the presence of *C. acutipennis* was confirmed or its absence could be satisfactorily assumed. In this context, absence means that the species does not make regular use of a particular vegetation type. This does not, however, preclude its occurrence on an irregular and/or infrequent basis. Observations were conducted both in the morning and evening hours.

At the San Jacinto study area, *C. acutipennis* was observed only in the desert scrub habitat on the east side of the mountains. Here it appeared to be quite common. Although extensive observations were made at higher elevations, not a single individual was recorded in any other vegetation type.

The lower elevations at the Laguna Mountain study site were of sufficient elevation to support chaparral. The nearest desert scrub vegetation occurs 15 miles to the east on the lower elevations of the Borrego Desert. *C. acutipennis* was not recorded at this study site.

On the west side of the Sierra San Pedro Mártir, the vegetation changes with increasing elevation, from coastal sage scrub to chaparral and then directly to coniferous forest (Anthony 1893-94). *C. acutipennis* was observed as high as 1300 ft in the coastal sage scrub vegetation type. The species did not appear to be common even at the lower elevations and was not recorded in any of the higher vegetation types.

Anthony's (1893-94) report of the species at 7200 ft was probably of an accidental. The likelihood of this becomes more apparent when it is realized that his locality is only 10 miles west of the eastern edge of this mountain mass. Here the mountains drop precipitously to nearly sea level, where the vegetation is distinctly desert scrub.

These field investigations indicate that *C. acutipennis* is truly a lowland inhabitant.

It is confined almost entirely to desert scrub vegetation in its allopatric range in the southwestern United States and northern Baja California. Habitats at higher elevations are not utilized to any great extent even in areas where its congener, *C. minor*, is absent.

Sympatry. Within the sympatric distribution, *C. minor* is generally limited to the higher elevations; it occurs in most mountain ranges and the adjacent foothills of the southwestern United States. *C. acutipennis* is abundant over the desert lowlands, seldom occurring in mountains above the upper edge of desert vegetation. Personal observations made in and adjacent to the Sierra Madre Occidental west of Durango, México, and the Sacramento, San Andres, and Black mountains of New Mexico indicated that this pattern seems to be generally widespread. In addition, many references suggesting this kind of habitat distribution appear in the literature (Grinnell 1928; Miller 1951; Selander 1954; Ligon 1961; Phillips et al. 1964; Hubbard 1970).

DISCUSSION OF HABITAT UTILIZATION

The term habitat displacement has been applied (Raitt and Hardy 1970) to situations where the breadth of habitat utilization of a species is narrowed in sympatry under the competitive influence of a second species. Habitat displacement may be considered a means of reducing competition between ecologically similar species. This displacement is a two-way exclusion when the breadth of habitat utilization of each species is narrowed under the influence of a competing species. Alternately, the displacement may be a one-way exclusion when the breadth of habitat utilization of only one species is reduced as a direct result of the presence of a second competing species.

Results just presented indicate that the breadth of habitat utilization of *C. minor* is decreased within the sympatric distribution while that of *C. acutipennis* seems unchanged. While physiological factors certainly determine general range differences, it would appear that the habitat differences demonstrated by these species within the study area are the result of other factors. These habitat relationships suggest that the presence of *C. acutipennis* precludes use of lowland habitats by *C. minor* within the sympatric distribution. Therefore habitat displacement appears evident. Since only the habitat range of *C. minor* is affected, the displacement is a one-way exclusion, with *C. acutipennis* maintaining itself on the lowlands in the face of

potential infringement from the upland-inhabiting *C. minor*.

Potential competitors must be effectively in contact both spatially and temporally in order for competition to occur; therefore, the effectiveness of habitat displacement in reducing competition is dependent on the fidelity of the species to their respective habitats. When habitat isolation breaks down and the species come into contact, the competitive interactions which have necessitated habitat displacement may be expected to operate strongly. The amount of interspecific interaction which results from imperfect habitat isolation is apparently quite variable. In their study of *Catharus occidentalis* and *C. frantzii*, Raitt and Hardy (1970) found that in areas where these species demonstrate habitat displacement their fidelity to respective habitats is very high, and although both species live in close association, no interspecific interactions were observed. This exclusiveness in habitat selection and consequent successful isolation are not apparent in these nighthawks. Selander (1954) reported that the "altitudinal separation apparently breaks down in Mexico . . ." between *C. minor* and *C. acutipennis*; however, he gave no further information. Two areas were located in southern New Mexico where this separation does break down; i.e., where both species breed in the same area. These localities are along the edges of mountain ranges in which *C. minor* is a summer resident. Here, both species apparently breed in close proximity. Intensive field observations and collections were made in these areas and the data are presented in the appropriate sections to follow.

TERRITORIAL SYSTEMS

Common Nighthawks generally maintain large, well-defined aerial territories. Those measured by Armstrong (1965) varied from 4.14 to 22.80 ha, which agrees with the general observations made in this study in southern New Mexico. Some exceptions to this general case have been reported in the literature. Gross (1940) recorded semi-colonial nesting of *C. minor*, with nest sites spaced from a few to 25 m apart; he felt that this was a result of a scarcity of nesting sites rather than of social attraction. Sutherland (1963) found 16 nests spaced about 73 m apart on a 10-ha flat. He pointed out that because the birds fed elsewhere, there was much territorial trespassing with consequent strife. No cases of aggregated nesting were observed during this study.

The territorial boundaries of *C. minor* are generally reasserted at the onset of each of the two daily activity periods. The male spends a period of time calling and displaying, often very high over the territory. It is the male that executes, mostly in the vicinity of the nest (Gross 1940; Weller 1958; Sutherland 1963), the precipitous dive that concludes with a booming sound. The female is generally much less conspicuous but may join the male in excluding intruders from the territory. When an intruder enters a territory, generally the frequency of the calls uttered by the defending male increases markedly while it flies toward the intruder. If the calls and the approach are not sufficient to exclude the intruder, then the defending bird may actively pursue the intruder, or climb high over it and dive toward it with or without the typical boom. The actual pursuit of an individual seemed to be the most intense response.

Observations made in an area where both species breed indicated that *C. minor* spends considerably more time excluding *C. acutipennis* from territories than excluding members of its own species. *C. minor* seemed to avoid trespassing onto adjacent territories even when several territories were juxtaposed. Although encounters along borders of territories were not uncommon, deep territorial penetration by conspecifics was seldom observed. Within the area of habitat overlap, *C. acutipennis* seemed to respond very little to the calls and dives of a defending *C. minor*, leaving a territory only if actually pursued. Of 17 actual pursuits observed where positive identification could be made, 13 were *C. minor-C. acutipennis* interactions, while only 4 were *C. minor-C. minor* interactions.

The territorial defense of *C. acutipennis* is much less conspicuous than that of *C. minor* and may, in fact, play a much less prominent role in the breeding of this species. I observed only one consistent response which could be construed as territorial defense. This occurred when an intruding *C. acutipennis* would fly relatively close to a roosting individual. The roosting bird might or might not fly up and pursue the intruder for a short distance before returning to its roost.

DISCUSSION OF TERRITORIALITY

Territorial behavior can be demanding in time, energy, and increased predation rates. The occurrence of territoriality throughout a wide variety of birds suggests that the advantages must generally outweigh these dis-

advantages. Because *C. minor* engages in territorial delimitation and defense in the air, predation rates are probably not appreciably affected by its territorial habit. In a crepuscular species such as *C. minor*, the time and energy demands of territorial defense could be particularly important. Certain mechanisms have evolved to minimize these. Feeding is generally done on or near the territory. This would be an effective means of minimizing or eliminating the time and energy required to travel to distant feeding sites, provided that territories with sufficiently high concentrations of food were available. As previously stated, there are exceptions to this pattern (Phillips et al. 1964; Sutherland 1963; Gross 1940); however, these situations no doubt arise from local peculiarities of suitable nest site locations and the available food supply. Another adaptation to territoriality is shown in the intraspecific respect of territory boundaries. This would serve to reduce the time and energy expenditure in territorial defense.

In *C. acutipennis* the role of territoriality is reduced while other mechanisms are substituted to fulfill the needs of the species. Since food and water in many of the habitats utilized by *C. acutipennis* are highly dispersed, the benefits of territoriality are superseded by the need to wander over great distances in search of these resources. Maintenance of the pair bond possibly is furthered by the tendency for this species to forage in pairs or family groups. Also the quiet trill uttered almost continuously by a foraging pair probably serves as a means of individual recognition and may also contribute to pair bond maintenance. Since little time is spent in territorial defense, more time can be devoted to foraging and hence greater distances can be covered. Also, nest site selection need not be based on the availability of food in the immediate vicinity because feeding often takes place some distance from the nest.

FOOD HABITS

In areas of habitat overlap, both species have access to the same resources. Thus, any differences in diets between the species would reflect differences in feeding adaptations. A comparative study of the diets and foraging behavior was undertaken to investigate these differences in the food niches and to provide insight into the potential competition for food. In an area of habitat overlap in southern New Mexico, a series of specimens of both

species was collected for stomach content analysis.

FORAGING PERIODICITY AND BEHAVIOR

Comparisons of the feeding periodicity were made by relating the per cent body weight of stomach contents of the specimens to the time of collection in minutes of deviation from sunset. These data are presented in figure 2. Active *C. minor* males were collected as early as -62 min, but the first actively feeding individual was not collected until -18 min, a full 44 min later. Females of this species and both sexes of *C. acutipennis* failed to show this pattern. Instead, indications of the initial stages of feeding were shown among the earliest collected specimens.

In the field, sexual determinations of *C. minor* were based on the less conspicuous and less aggressive posture of the female. These observations were confirmed by collection. *C. minor* males spend the early portions of their activity period in territory delimitation and defense. This includes those times when the males can be observed flying high over a territory calling and occasionally diving. It seems that little feeding actually takes place during these initial portions of the activity period. Often later in the activity period a calling bird might disappear for a short period and subsequently be observed flying very close to the ground. Although it is not possible to ascertain just when feeding is taking place, it seems likely that most feeding actually takes place during these periods, at comparatively low heights. Female *C. minor* were, in general, much less conspicuous than males, but were observed at various times during the activity period flying just above the creosote bushes, presumably engaged in feeding.

There does not seem to be a general difference between these species in foraging height. Such a difference might be inferred from frequent observations of *C. minor* flying at considerable heights, but my observations would indicate that these high flying individuals are usually displaying males and that foraging is generally carried on at much lower heights. As will be pointed out subsequently, the "preferred" food sources of both species are insect swarms, and when these swarms are available, both species feed on the same insects. It is possible that the two species feed on the same insects, but from different heights above the ground. However, a more plausible explanation is that both species of nighthawks feed on insect swarms from wherever they are available.

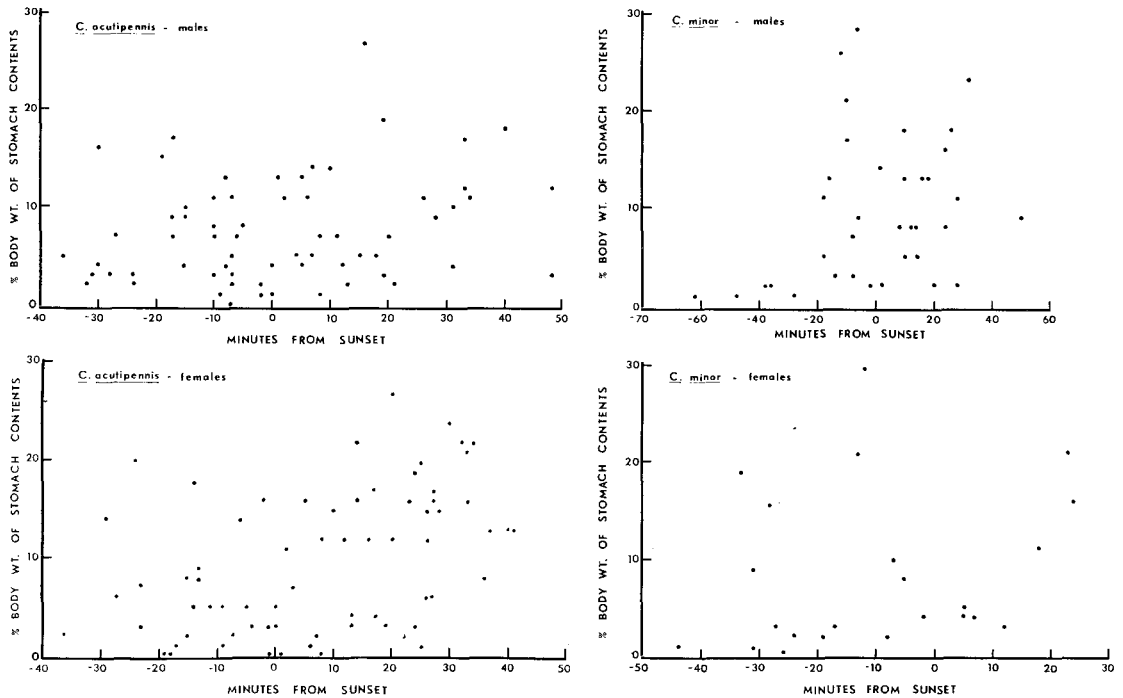


FIGURE 2. Per cent body weight of stomach contents versus time of capture in minutes deviation from sunset.

DIET

Both species appear to be opportunistic feeders, taking that food which is most abundant and most easily captured. There were no apparent differences in the size range of food items taken. During certain times of the year, the diets of both species often contained similar proportions of both the largest (Cicadidae) and the smallest (Cicadellidae) prey items.

Tables 1 and 2 list, by weekly intervals, the weight and the per cent of the total weight of prey within each insect family found in the Taylor Well specimens. Also indicated is the food diversity based on weights within each insect family, using Shannon's measure of information (Shannon 1949). Certain of the weekly sample sizes are small; however, as there was very little variation between specimens in the composition of stomach contents within any time interval, separation of the data into weekly intervals seemed justified.

DISCUSSION OF FOOD HABITS

A number of methods for the measure of niche overlap have been suggested recently (Pico et al. 1965; MacArthur and Levins 1967; Cody 1968; Levins 1968; Schoener 1968). Horn (1966) presented a method based on Shannon's (1949) measure of information

which seemed particularly useful in measuring the overlap of food niches in these species of nighthawks. The index varies from 0 at no overlap to unity at complete overlap. In addition, niche breadth can be measured using the formula H/H_{\max} (Horn 1966; Levins 1968; Willson 1970) where H is Shannon's diversity measure and H_{\max} equals log of N (N = the number of categories). This index also varies from 0 to 1 as the food niche progresses from specialized to generalized.

Figure 3 indicates the per cent contribution to the total diet for each sex of the seven quantitatively most important insect families. To adjust these values for the variation in the numbers of specimens collected within the weekly intervals, the average diets for each weekly interval were calculated separately. These averages were then pooled to obtain the per cent contribution of each insect family to the total diet. These differences in food overlap were evaluated quantitatively using Horn's index (1966).

Comparisons were made between the sexes of each species and between the species as a whole. The levels of overlap between the sexes of *C. acutipennis* (0.90) and between the two species (0.88) were about the same. However, there is considerably less overlap between the sexes of *C. minor* (0.72). Thus the divergence in food niches between the sexes is greater

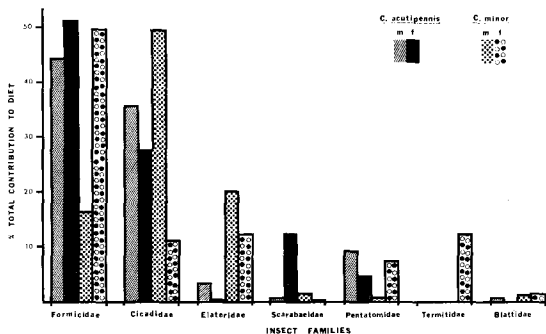


FIGURE 3. Per cent contribution by weight of the seven quantitatively most important insect families to the total diet of each sex in *C. minor* and *C. acutipennis*.

for *C. minor* than for *C. acutipennis*. This divergence in *C. minor* is not surprising considering the differences in behavior (territorial defense and feeding periodicity) between the sexes.

Figure 4 shows the changes through time in the proportional contribution to the total diet of the five quantitatively most important insect families. Divergence in diet between the species is apparent for the weeks 7-13 June, 5-11 July, and 12-18 July. During the remaining weekly intervals, the diets were very similar. The overlap in diet between the species was evaluated during each weekly period using Horn's index (1966). These values and the indices of specialization are given in figure 5 for the weekly periods throughout the study.

To understand the variations in these values, foraging techniques and environmental con-

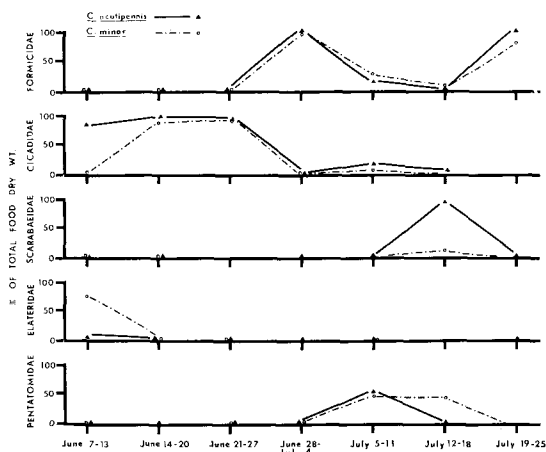


FIGURE 4. Weekly changes in the per cent of total food dry weight of the five quantitatively most important insect families represented in the stomach contents of *C. minor* and *C. acutipennis*.

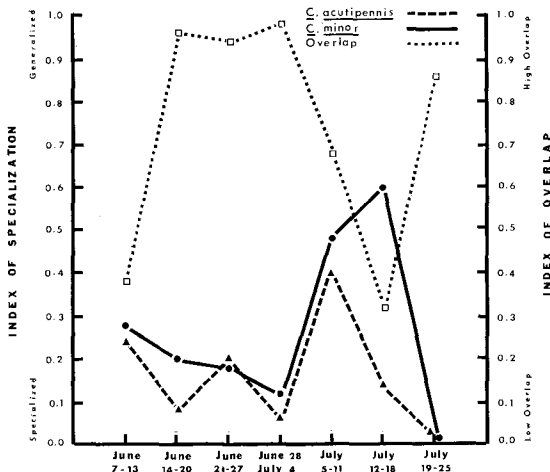


FIGURE 5. Levels of food overlap between *C. minor* and *C. acutipennis* and changes in feeding specialization which occurred during the period of investigation.

ditions must be considered. Stomach contents from both species of nighthawks showed that often one or two species of insects made up 90-100% of the total food weight. This would suggest that, when feeding, these nighthawks normally seek, either actively or passively, areas where there are high concentrations of insects, e.g., swarms of flying ants or large numbers of emerging cicadas. This type of swarm feeding would seem to be very efficient energetically. In seeking out these areas, casual feeding no doubt would occur. Thus, those birds which are successful in finding areas of high insect concentrations would show a high level of feeding specialization and those not finding concentrations would show very low levels.

During the week of 7-13 June, there was low overlap between the species, but relatively high levels of specialization. This indicates that, although the species fed on different insects, they were both able to accomplish similar amounts of swarm feeding. From 5-11 July, both species showed more generalized feeding compared with the previous weeks, indicating that insect swarms were utilized less. In the following week, 12-18 July, the feeding of *C. acutipennis* became more specialized while *C. minor* showed a yet more generalized feeding pattern. Thus, during this period, *C. acutipennis* was able to find and utilize insect swarms as a food source, while *C. minor* was unable to do so.

As shown in tables 1 and 2 and by Caccamise (1971), flying ants often make up a large proportion of the diet of both nighthawks and are probably selected over most other food

TABLE 1. Stomach contents from Taylor Well specimens of *C. minor*: weight (g) and per cent weight of items in each food category.

Insect groups ^a	7-13 June (n=5)		14-20 June (n=2)		21-27 June (n=11)		28 June-4 July (n=3)		5-11 July (n=3)		12-18 July (n=4)		19-25 July (n=3)	
	wt.	% wt.	wt.	% wt.	wt.	% wt.	wt.	% wt.	wt.	% wt.	wt.	% wt.	wt.	% wt.
Aradidae	— ^b	—	—	—	—	—	—	—	—	—	0.020	1.7	—	—
Coreidae	—	—	—	—	0.196	1.2	—	—	—	—	0.002	0.2	—	—
Corixidae	—	—	—	—	—	—	—	—	0.008	0.2	—	—	—	—
Cydnidae	—	—	0.155	2.8	0.022	0.1	0.007	0.1	0.023	0.6	0.009	0.7	0.002	0°
Lygaeidae	0.043	0.4	—	—	0.002	0	0.001	0	0.038	0.9	0.019	1.6	—	—
Miridae	0.032	0.3	—	—	0.003	0	—	—	0.003	0.1	—	—	—	—
Nabidae	0.021	0.2	0.003	0.1	0.006	0	—	—	0.030	0.73	0.005	0.4	—	—
Neididae	0.001	0	—	—	t ^c	0	—	—	—	—	—	—	—	—
Pentatomidae	0.042	0.4	—	—	0.300	1.8	0.123	1.5	2.024	49.6	0.508	43.0	—	—
Reduviidae	—	—	—	—	—	—	0.021	0.3	—	—	0.013	1.1	—	—
Scutelleridae	—	—	—	—	0.017	0.1	—	—	—	—	0.006	0.5	—	—
Cercopidae	0.007	0.1	0.029	0.5	0.019	0.1	—	—	0.002	0	—	—	—	—
Cicadellidae	0.041	0.4	0.001	0	0.018	0.1	0.008	0.1	0.052	1.3	0.016	1.4	—	—
Cicadidae	0.130	1.2	4.956	88.7	14.676	87.5	0.128	1.6	0.283	6.9	—	—	—	—
Delphacidae	—	—	0.007	0.1	—	—	—	—	—	—	—	—	—	—
Dictyopharidae	—	—	—	—	—	—	—	—	0.004	0.1	—	—	—	—
Membracidae	0.005	0	—	—	0.018	0.1	—	—	—	—	—	—	—	—
Chrysopidae	t	0	—	—	—	—	—	—	—	—	—	—	—	—
Myrmeleontidae	0.139	1.2	—	—	0.006	0	—	—	—	—	—	—	—	—
Macrolepidoptera	0.014	0.1	—	—	—	—	—	—	—	—	—	—	—	—
Microlepidoptera	0.025	0.2	0.002	0	0.028	0.2	0.002	0	0.100	2.4	0.006	0.5	—	—
Noctuidae	0.014	0.1	—	—	—	—	—	—	t	0	0.001	0.1	—	—
Alleculidae	0.003	0	—	—	—	—	—	—	0.106	2.6	—	—	—	—
Bruchidae	0.045	0.4	0.008	0.2	0.017	0.1	—	—	—	—	0.004	0.4	—	—
Carabidae	—	—	—	—	0.008	0.1	0.012	0.2	0.050	1.2	0.097	8.2	—	—
Cerambycidae	—	—	0.019	0.3	—	—	0.008	0.1	—	—	—	—	—	—
Chrysomelidae	0.345	3.0	—	—	0.003	0	—	—	0.006	0.1	—	—	—	—
Cicindelidae	0.013	0.1	—	—	—	—	—	—	—	—	—	—	—	—
Coccinellidae	—	—	0.017	0.3	—	—	—	—	—	—	—	—	—	—
Curculionidae	0.013	0.1	—	—	—	—	—	—	0.001	0	0.001	0.1	—	—
Elaeuteridae	8.900	79.0	0.077	1.4	0.804	4.8	0.078	1.0	0.123	3.0	0.245	20.7	—	—
					0.077	0.5	—	—	0.061	1.5	—	—	—	—

TABLE 1. *Continued.*

Insect groups ^a	7-13 June (n = 5)		14-20 June (n = 2)		21-27 June (n = 11)		28 June-4 July (n = 3)		5-11 July (n = 3)		12-18 July (n = 4)		19-25 July (n = 3)	
	wt.	% wt.	wt.	% wt.	wt.	% wt.	wt.	% wt.	wt.	% wt.	wt.	% wt.	wt.	% wt.
Histeridae	—	—	—	—	0.085	0.5	—	—	—	—	—	—	—	—
Meloidae	—	—	0.230	4.1	0.101	0.6	—	—	—	—	—	—	—	—
Scarabaeidae	0.346	3.0	0.044	0.8	—	—	—	—	—	—	0.129	10.9	—	—
Staphylinidae	0.001	0	—	—	—	—	—	—	t	0	—	—	—	—
Tenebrionidae	0.053	0.5	—	—	—	—	—	—	—	—	—	—	—	—
Diptera	0.006	0.1	—	—	0.001	0	—	—	—	—	0.002	0.2	—	—
Chamaemyiidae	—	—	—	—	0.001	0	—	—	—	—	—	—	—	—
Dolichopodidae	—	—	—	—	—	0	—	—	—	—	—	—	—	—
Empididae	—	—	—	—	t	—	—	—	—	—	—	—	—	—
Muscidae	0.004	0	—	—	0.001	0	—	—	—	—	—	—	—	—
Tachinidae	0.004	0	—	—	0.002	0	—	—	0.001	0	—	—	—	—
Tephritidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Andrenidae	—	—	—	—	0.001	0	—	—	—	—	—	—	—	—
Braconidae	0.005	0	—	—	—	—	—	—	0.001	0	—	—	—	—
Formicidae	0.004	0	—	—	—	—	—	—	0.001	0	—	—	—	—
Ichneumonidae	0.004	0	0.004	0.1	0.294	1.8	7.662	95.2	1.102	27.0	0.080	6.8	6.657	77.2
Megachilidae	—	—	—	—	0.001	0	—	—	0.006	0.1	—	—	—	—
Stephanidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Tenthredinidae	—	—	0.014	0.25	0.001	0	—	—	—	—	—	—	—	—
Tiphiidae	—	—	0.004	0.1	—	—	—	—	—	—	—	—	—	—
Vespidae	0.005	0	—	—	—	—	—	—	—	—	—	—	—	—
Acrididae	0.155	1.4	—	—	—	—	—	—	—	—	—	—	—	—
Blattidae	0.843	7.5	0.016	0.3	0.070	0.4	—	—	—	—	—	—	—	—
Kalotermitidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Libellulidae	—	—	—	—	—	—	—	—	0.036	0.9	0.018	1.5	1.965	22.8
Total weight	11.26		5.59		16.77		8.05		4.08		1.18		8.62	
Food Diversity ^e		0.98		0.57		0.64		0.27		1.58		1.79		0.54

^a The level of identification was to family with the exception of Macrolepidoptera, Microlepidoptera, and Diptera.

^b Indicates that a food category was not represented in specimens from that time interval.

^c Indicates that per cent weight of a food category is less than 0.05.

^d Trace: less than 0.0005 g.

^e Based on Shannon's (1949) measure of information.

TABLE 2. Stomach contents from Taylor Well specimens of *C. acutipennis*: weight (g) and per cent weight of items in each food category.

Insect groups ^a	7-13 June (n = 11)		14-20 June (n = 10)		21-27 June (n = 10)		28 June-4 July (n = 9)		5-11 July (n = 8)		12-18 July (n = 5)		19-25 July (n = 8)	
	wt.	% wt.	wt.	% wt.	wt.	% wt.	wt.	% wt.	wt.	% wt.	wt.	% wt.	wt.	% wt.
Cydnidae	— ^b	—	0.069	0.3	—	—	0.026	0.1	0.096	0.8	—	—	—	—
Flatidae	—	—	—	—	—	—	—	—	—	—	0.002	0 ^c	—	—
Lygaeidae	0.004	0	0.004	0	—	—	—	—	0.145	1.2	0.290	3.4	—	—
Miridae	0.117	0.8	—	—	0.006	0.1	—	—	—	—	0.001	0	—	—
Nabidae	0.015	0.1	—	—	0.013	0.1	0.011	0.1	0.034	0.3	0.006	0.1	0.005	0
Neididae	—	—	—	—	—	—	—	—	—	—	0.002	0	—	—
Pentatomidae	0.007	0.1	0.014	0.1	0.039	0.4	0.058	0.3	6.962	55.9	0.045	0.5	—	—
Reduviidae	0.005	0	—	—	—	—	—	—	0.018	0.1	0.002	0	—	—
Cercopidae	0.005	0	0.036	0.2	0.002	0	—	—	0.005	0	—	—	—	—
Cicadellidae	0.034	0.3	0.003	0	0.038	0.3	0.008	0	0.352	2.8	t ^d	0	—	—
Cicadidae	11.925	80.7	22.072	96.5	9.757	86.4	0.233	1.1	2.444	19.6	—	—	—	—
Dictyopharidae	—	—	—	—	—	—	—	—	0.018	0.1	—	—	—	—
Membracidae	0.002	0	—	—	0.017	0.2	0.003	0	0.122	1.0	—	—	—	—
Myrmeleontidae	0.030	0.2	0.105	0.5	0.006	0.1	—	—	0.001	0	—	—	—	—
Macrolepidoptera	—	—	0.069	0.3	0.133	1.2	0.025	0.1	—	—	0.024	0.3	—	—
Microlepidoptera	0.049	0.3	0.032	0.1	0.045	0.4	0.004	0	0.005	0	—	—	—	—
Noctuidae	0.046	0.3	—	—	—	—	—	—	—	—	—	—	—	—
Anthicidae	—	—	—	—	—	—	—	—	—	—	0.001	0	—	—
Bostichidae	—	—	—	—	—	—	0.010	0.1	—	—	—	—	—	—
Bruchidae	0.011	0.1	0.006	0	0.031	0.3	0.004	0	0.009	0.1	0.001	0	—	—
Carabidae	0.018	0.1	—	—	0.008	0.1	0.002	0	0.157	1.3	0.006	0.1	0.024	0.2
Cerambycidae	0.036	0.2	0.031	0.1	—	—	—	—	0.032	0.3	—	—	—	—
Chrysomelidae	0.055	0.4	0.003	0	0.003	0	—	—	0.004	0	t	0	—	—
Coccinellidae	—	—	—	—	—	—	—	—	0.005	0	t	0	—	—
Curculionidae	0.050	0.3	0.041	0.2	0.055	0.5	0.005	0	0.008	0.1	—	—	—	—
Dytiscidae	—	—	—	—	—	—	—	—	—	—	0.002	0	—	—
Elaeteridae	1.652	11.2	0.048	0.2	0.340	3.0	0.235	1.2	0.007	0.1	—	—	—	—

TABLE 2. *Continued.*

Insect groups ^a	7-13 June (n = 11)		14-20 June (n = 10)		21-27 June (n = 10)		28 June-4 July (n = 9)		5-11 July (n = 8)		12-18 July (n = 5)		19-25 July (n = 8)	
	wt.	% wt.	wt.	% wt.	wt.	% wt.	wt.	% wt.	wt.	% wt.	wt.	% wt.	wt.	% wt.
Histeridae	0.069	0.5	0.108	0.5	0.029	0.3	—	—	0.020	0.2	—	—	—	—
Melandyridae	0.009	0.1	—	—	—	—	—	—	—	—	—	—	—	—
Meloidae	0.073	0.5	0.066	0.3	0.324	2.9	—	—	—	—	—	—	—	—
Mordellidae	—	—	—	—	—	—	0.002	0	—	—	—	—	—	—
Nitidulidae	—	—	—	—	—	—	—	—	0.001	0	—	—	—	—
Scarabaeidae	0.097	0.7	0.002	0	—	—	0.002	0	0.003	0	7.673	90.6	0.002	0
Scolytidae	—	—	—	—	—	—	—	—	0.009	0.1	—	—	—	—
Staphylinidae	0.001	0	—	—	—	—	—	—	—	—	t	0	0.009	0.1
Tenebrionidae	0.004	0	—	—	—	—	—	—	0.005	0	—	—	—	—
Diptera	0.027	0.2	—	—	0.007	0.1	—	—	—	—	—	—	—	—
Asilidae	—	—	—	—	0.200	1.7	—	—	—	—	0.004	0.1	—	—
Tachinidae	—	—	—	—	t	0	—	—	—	—	—	—	—	—
Braconidae	—	—	0.001	0	0.005	0	—	—	t	0	—	—	—	—
Formicidae	0.119	0.8	0.001	0	0.030	0.3	19.757	96.9	1.890	15.2	0.408	4.8	16.126	99.8
Ichneumonidae	0.002	0	0.010	0	0.001	0	—	—	—	—	—	—	—	—
Tiphidae	0.041	0.3	—	—	—	—	—	—	—	—	—	—	—	—
Vespidae	—	—	0.012	0.1	—	—	—	—	—	—	—	—	—	—
Acrididae	—	—	—	—	0.186	1.7	—	—	0.098	0.8	—	—	—	—
Blattidae	0.258	1.7	0.145	0.6	—	—	—	—	—	—	—	—	—	—
Libellulidae	0.015	0.1	—	—	0.015	0.1	—	—	0.006	0.1	—	—	—	—
Total weight	14.78		22.88		11.29		20.39		12.46		8.47		16.17	
Food Diversity ^e		0.85		0.24		0.71		0.19		1.36		0.42		0.02

^a The level of identification was to family with the exception of Macrolepidoptera, Microlepidoptera, and Diptera.

^b Indicates that a food category was not represented in specimens from that time interval.

^c Indicates that per cent weight of a food category is less than 0.05.

^d Trace: less than 0.0005 g.

^e Based on Shannon's (1949) measure of information.

sources. However, because of the near absence of rain showers in the vicinity of the collection site during the early portions of the summer of 1970, the emergence of ants was greatly restricted. The only significant shower prior to mid-July occurred on 1 July. Its effect can be seen in the peak in ant feeding (fig. 4) during the week of 28 June–4 July. Its effect was not long-lasting, as indicated by the precipitous decline in ant feeding in the following 2 weeks. The week of 19–25 July again showed a large increase in ant feeding as a result of a shower on 20 July. Thus, both species of nighthawks seem to respond very quickly to the availability of ants, substituting them when they are abundant for other food sources. When both the overlap between species and feeding specialization of *C. minor* were declining (5–18 July), there was a conspicuously low dependence by both species on what is often one of the most important food sources, flying ants. This would suggest that during this period food was scarce. Similar declines in overlap during periods of food scarcity were reported by Holmes and Pitelka (1968) for closely related species of sandpipers and by Zaret and Rand (1971) for tropical stream fishes.

FLIGHT AND AERODYNAMICS

Flight in *C. minor* and *C. acutipennis* is so intricately woven into the fabric of their existence that any ecological comparison would be incomplete without studies on flight characteristics. Food and water are obtained solely on the wing. Courting and mate selection are carried out in flight (Miller 1925; Miller 1937). *C. minor* and, to a lesser extent, *C. acutipennis* establish and maintain territories through displays performed mainly in flight.

A comparative study avoids many of the inherent difficulties in the analysis of flight mechanics. This is because primary interest lies in relative differences as opposed to absolute determinations. In comparing the aerodynamics of these nighthawks, those features of morphology and flight mechanics were selected for study which were both easy to measure and likely to provide comparative information on the ecological relationships of these species.

FLIGHT CHARACTERISTICS

There are subtle but consistent differences in flight pattern between these species of nighthawks; however, there is also considerable

overlap. It is not uncommon to observe either species engaged in a flight pattern more typical of the other species than of its own. In characterizing these flight patterns, it is only possible to speak in terms of different tendencies for each species, realizing that exclusive characteristics are uncommon.

C. acutipennis is generally a slower and more maneuverable flier than *C. minor*. When foraging, its flight can be quite erratic, with much bobbing and weaving. *C. minor* generally flies noticeably faster, with considerably fewer course changes. Both species are capable of prolonged gliding, but there are marked differences in glide sequencing during periods of flapping flight. In *C. acutipennis* each series of several wingbeats is generally followed by a glide of varying duration, followed again by a series of wingbeats. This alternation of flapping and gliding is perhaps the most characteristic feature in the flight pattern of *C. acutipennis*. Measurements of the proportionate amount of time spent in gliding flight were obtained by using a tape recorder to record verbally the alternation of flapping and gliding flight. The tapes were later played back and the flight sequences timed with a stop watch. Out of a total of 2167 sec of observation obtained on four separate occasions, *C. acutipennis* spent 41–55% of its foraging time in gliding flight.

C. minor generally flaps continuously without regular interspersions of glide phases; therefore, timed measurements of this species were not made. When gliding does occur, it often lasts for extended periods. During these periods, the birds may often be engaged in soaring flight, riding thermals and up-drafts which must be common in many of the breeding areas.

Both species are able to hover, at least to a limited extent. Hovering was regularly observed at various ponds used as water sources. Individuals fly to these ponds, often several at a time, hover over the water surface, drink, and then fly off.

WINGBEAT COMPONENTS

In order to compare the individual components of the wingbeat, 16-mm motion pictures were taken of both species in flight. All pictures were taken at 64 fps under similar conditions of wind and temperature. Each wingbeat was separated into three components: down-stroke, up-stroke, and glide-phase. The time sequencing of these components is illustrated in figure 6. It should be noted that the glide component interrupts the up-stroke, with the

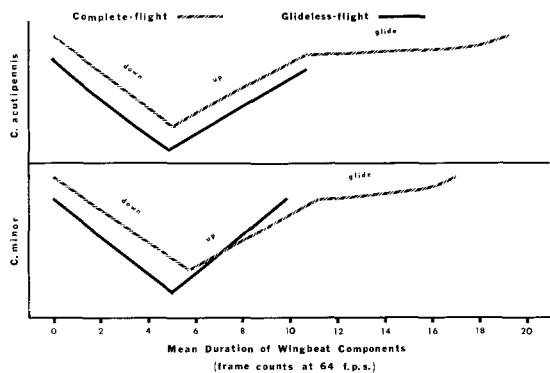


FIGURE 6. Duration of wingbeat components during complete-flight and glideless-flight in *C. minor* and *C. acutipennis*.

major portion of the up-stroke occurring prior to the glide. It was necessary to include the second and shorter portion of the up-stroke with the glide because of the difficulty involved in recognizing the difference between the two. The duration of each wingbeat component was determined by counting the frames on which a particular component occurred. Since the time resolution was limited by the film speed, the data were left as frame counts rather than converted into units of time. Statistical comparisons were made using a standard "student's t-test" for unpaired data.

Two types of flight were recognized and analyzed separately. The first, complete-flight, was comprised of all three wingbeat components. In the second type, glideless-flight, the glide component was absent or sufficiently short so that its resolution was not possible at the frame speed used.

The duration of the wingbeat in glideless-flight was not statistically different between the species. In complete-flight (table 3) the duration of each wingbeat was significantly longer in *C. acutipennis*, indicating a lower frequency of wingbeats. Comparisons made between the sums of the down-stroke and up-stroke for each species were not significant. Thus, the difference in the total length of the wingbeat of *C. acutipennis* is due to its longer glide-phase.

In order to compare the active portions of the wingbeat in the two flight types, the duration of the down- and up-strokes were summed for complete-flight and these compared with the duration of the total glideless-flight wingbeat. In *C. acutipennis* the mean length of the wingbeats in glideless-flight was very similar to the sums of the down-stroke and up-stroke in complete-flight. In *C. minor* the

TABLE 3. Mean duration of wingbeat components in *C. minor* and *C. acutipennis*.

	n	Continuous		Glideless		
		\bar{x}	SE	n	\bar{x}	SE
<i>C. minor</i>	292			136		
Down		5.8	0.1		5.0	0.1
Up		5.6	0.4		5.0	0.2
Glide		5.8	0.3		—	—
<i>C. acutipennis</i>	170			29		
Down		5.3	0.1		4.9	0.2
Up		5.5	0.1		5.8	0.3
Glide		8.7	1.1		—	—

two components of glideless-flight were significantly shorter than the sum of the down- and up-stroke in complete-flight. Apparently *C. minor* alters the duration of the powered portion of the wingbeat depending on its mode of flight, and hence can alter its flight speed. The mean difference in *C. minor* between glideless-flight and the sum of the down- and up-strokes in complete-flight is 12.3%. Schaefer (1967) suggests that wingbeat is at a resonant frequency and generally does not vary more than 10%. This relationship appears not to apply for either species. *C. minor* alters its wingbeat frequency in order to change flight speed and both species alter wingbeat frequency by inserting a glide-phase of variable length into the wingbeat.

WING MORPHOLOGY

Wing and tail loading. Determinations of wing and tail loading were made on 10 *C. acutipennis* and 14 *C. minor*. Methods employed in obtaining surface areas were similar to those described by Owre (1967:8, 48). The alula is relatively small in both species and is probably unimportant during flight; it was, therefore, not included in wing area determinations. Measurements of wing area, tail area, and weight are summarized by Caccamise (1971). Determinations of wing and tail loading based on these data are presented in table 4.

Sexual dimorphism in wing and tail loading was not indicated for either species. The wing areas obtained for *C. minor* agree quite closely with those presented for this species by Poole (1938). The mean wing loading of *C. acutipennis* (table 4) is 27.4% less than that of *C. minor*. The mean loading of the combined wing and tail surfaces of *C. acutipennis* is 25.7% less than that of *C. minor*. By including tail area in these determinations, the loading decreases 17.6% in *C. acutipennis* and 19.3%

TABLE 4. Wing and tail loading in *C. minor* and *C. acutipennis*.

	n	Wing loading (g/cm ²)			Wing and tail loading (g/cm ²)		
		\bar{x}	SE	Range	\bar{x}	SE	Range
<i>C. minor</i>							
male	8	0.218	0.011	0.185-0.276	0.175	0.008	0.147-0.218
female	6	0.204	0.010	0.175-0.238	0.166	0.008	0.145-0.195
male and female	14	0.212	0.008	0.175-0.276	0.171	0.006	0.145-0.218
<i>C. acutipennis</i>							
male	5	0.152	0.010	0.130-0.190	0.125	0.008	0.110-0.158
female	5	0.156	0.006	0.138-0.173	0.130	0.006	0.112-0.145
male and female	10	0.154	0.006	0.130-0.190	0.128	0.005	0.110-0.158

in *C. minor*. The 1.7% difference in these values suggests that the tail of *C. minor* contributes slightly more, proportionately, to the total aerodynamic surface of this species than does the tail of *C. acutipennis*.

Aspect ratios. Aspect ratios can provide insight into the general flight characteristics of a species by giving some indication of the functional shape of a wing. Aspect ratios were calculated by dividing the square of the wing span by the surface area of the wing (Landé 1945). As indicated in table 5, the aspect ratios in *C. minor* were significantly greater than those of *C. acutipennis*.

Main elements of the wing skeleton. Measurements of the wing bones were made on 23 *C. acutipennis* (10 male, 13 female) and 16 *C. minor* (12 male, 4 female). When corresponding elements from both wings were available, the average of the bones from both sides were used; otherwise, one measurement was assumed to be adequate. These measurements are presented in table 6.

Sexual dimorphism, as indicated by significance at the $t_{0.05}$ level, was apparent in the absolute lengths of all the wing bones in *C. acutipennis*, but in none for *C. minor*. Sexual dimorphism in the relative lengths of the wing bones was significant only in measurements of the carpometacarpus plus phalanx 1, digit III (after Montagna 1945), in *C. acutipennis*.

In comparing the relative lengths of the wing bones between the species, significance was indicated in two of the three ratios. In both sexes of *C. acutipennis*, the relative length of the carpometacarpus plus phalanx 1, digit III, was significantly longer than in *C. minor*. Differences in ulna ratios were not significant.

From a functional standpoint, these differences are difficult to interpret. The general size relationships of both species (humerus < ulna < manus) are most like the Falconidae as presented by Engels (1941). Certain superficial similarities in flight between these nighthawks and the Falconidae are apparent, but it is difficult to postulate specific relationships between skeletal configuration and flight.

DISCUSSION OF FLIGHT AND AERODYNAMICS

The differences in flight pattern between the species correspond in many respects to the differences which might be predicted from a theoretical aerodynamic standpoint based on morphological comparisons. In the following discussion, the wing is treated as a fixed airfoil as it might serve during gliding flight. The main aerodynamic properties of an airfoil are determined by essentially three characteristics: planform (the wing contour viewed from above); profile (cross section); and

TABLE 5. Span (mm) and aspect ratio (span²/surface area) of *C. minor* and *C. acutipennis*.

	n	Span (b)			Aspect ratio (b ² /S)		
		\bar{x}	SE	Range	\bar{x}	SE	Range
<i>C. minor</i>							
male	8	536.0	5.5	508-554	8.5	0.1	8.1-8.9
female	6	544.0	13.3	504-603	8.2	0.1	7.7-8.5
<i>C. acutipennis</i>							
male	5	512.0	11.3	475-539	7.8	0.1	7.4-8.0
female	5	486.2	5.0	477-504	7.6	0.1	7.3-7.7

TABLE 6. Measurements of the main wing bones of *C. minor* and *C. acutipennis*.

	n	Humerus			Ulna			Manus		
		\bar{x}	SE	Range	\bar{x}	SE	Range	\bar{x}	SE	Range
<i>C. minor</i>										
male	12	40.6	0.28	38.9-41.7	50.0	0.34	48.5-52.4	53.4	0.44	51.2-56.3
female	4	41.1	0.55	40.0-42.5	50.3	0.44	49.0-51.2	53.9	0.26	53.3-54.5
<i>C. acutipennis</i>										
male	10	35.6	0.28	34.1-36.9	46.1	0.37	43.5-47.9	51.1	0.50	48.2-53.9
female	12	34.8	0.19	33.9-36.2	45.0	0.36	43.7-47.3	48.8	0.38	47.0-51.5

aspect ratio (span/chord or in the case of nonrectangularity, span²/surface area). Similarity between the species in planform was apparent in the wing outlines which were made for surface area determinations. Because of the complexities of measurement, parameters of profile were not determined empirically; but based on general morphological similarities of the species, disparity would not be expected. The aspect ratios are indicated in table 5.

From the formula discussed by Landé (1945)

$$L \cdot L/D = 0.5\rho V^2 S (b^2/S)$$

(L = lift, D = drag, ρ = air density, V = velocity, S = surface of the wing, b = span), it is apparent that lift can be increased either by increasing velocity (V) or aspect ratio (b^2/S). Because the wing loading of *C. minor* is considerably greater than in *C. acutipennis*, additional lift must be provided. Assuming that planform and profile are essentially the same, this lift could be furnished by increasing flight velocity, by a larger aspect ratio, or by a combination of both. *C. acutipennis* has a much lighter wing loading than *C. minor*, and therefore, would be expected to fly much slower and/or have a lower aspect ratio. Both of these expectations are fulfilled. Generally, the flight speed of *C. acutipennis* seems to be considerably slower than that of *C. minor*, and the aspect ratio is smaller.

DISCUSSION AND CONCLUSIONS

It has been suggested that *C. acutipennis* is the superior competitor in desert habitats of the southwestern United States. Certain differences in feeding habits, behavior, and flight characteristics have also been indicated. Remaining to be discussed are how these differences confer a competitive advantage to *C. acutipennis* and what mechanisms provide for exclusion of *C. minor* from the preferred habitats of *C. acutipennis*.

ADAPTATIONS

C. acutipennis. Within the desert habitats utilized by *C. acutipennis*, sources of food and water are generally quite ephemeral, irregularly dispersed, and/or of low density. Certain adaptations are apparent in *C. acutipennis* which would provide for the efficient utilization of resources under these conditions.

C. acutipennis does not actively patrol a well-defined territory, but roams over considerable distances in search of food and water. At local concentrations of these resources, many individuals may congregate and jointly harvest the resource with very little aggression.

The necessity for foraging over large areas would seem to be incompatible with pronounced territoriality. During a major portion of the study period, both species were seemingly able to obtain sufficient food at the study site within the sympatric distribution. When food, by inference, became scarce, the competitive superiority of *C. acutipennis* became evident in its ability to swarm feed at a time when *C. minor* was unable to do so. Success at locating food by active searchers such as these nighthawks is directly related to two factors: food density and the area covered during a particular search. When food density declines, the search area must be increased, or a less suitable food used in order to maintain feeding success at a constant level. Since *C. acutipennis* does not remain on a territory for defense or delineation, this species is able to find and utilize food sources some distance from the nesting or roosting site.

Other mechanisms have evolved to replace some of those functions generally ascribed to territoriality. There seems to be a tendency for this species to forage in what appear to be pairs or family groups. In a species which is not highly territorial, but is very mobile, this could serve to protect the pair bond and/or prevent copulation with strange males. Since solitary individuals are not uncommon,

this tendency to forage in groups may vary through the breeding cycle.

Flight characteristics in *C. acutipennis* also seem to be closely related to the habit of this species to travel considerable distances when foraging. The relatively high aspect ratio of the wing, the low wing loading, and the high percentage of time spent in gliding flight would suggest an energetically conservative flight mode. This would provide for long foraging trips at low energetic costs.

In comparing the flight modes and wing morphologies of these two species of night-hawk, it was shown that *C. acutipennis* generally flies slower and has a wing with a lower aspect ratio and a lower wing loading. These factors would provide for greater flight maneuverability than in *C. minor*. Within shrub and/or grass-dominated habitats, *C. acutipennis* often feeds very close to the vegetation surface, with the birds often flying among the shrubs rather than above them.

C. minor. This species is strongly territorial, spending a major portion of its activity period within its territorial boundaries. In such territorial species, it would seem advantageous for individuals to spend minimum amounts of time away from their territories. Observations indicated that *C. minor* males spend a major part of the activity period in conspicuous display, calling and circling over a territory. Commonly, an individual may disappear from sight for a short period and then, suddenly, reappear calling and displaying. The significance of these periods of absence is not fully understood, but it seems likely that the birds are feeding or flying to nearby water sources to drink. In any event, they are generally absent for only short periods of time, and therefore probably accomplish most or all feeding on or near their territories. This would indicate that these territories are generally sufficiently large and productive to satisfy the food requirements of a pair of nighthawks. During periods of normal insect abundance, *C. minor* is probably well able to satisfy its dietary requirements in most desert habitats.

Although the function of territoriality in birds has been a point of much dispute, there is no doubt that a species must pay a high premium for territorial maintenance. As pointed out by Orians and Willson (1964), "conspicuous advertising by territorial males results in increased predation rates and requires increased energy intake while reducing the time available for feeding, resting, preening, and care of the offspring. . . ." A species such as *C. minor*, which has developed a

strongly territorial habit, with most feeding done within the territorial boundaries, would seem best adapted to conditions where food dispersion was relatively uniform both spatially and temporally. Armstrong (1965), in his study of the breeding home range of *C. minor*, found that "there was no significant correlation between home range size and density of trees or photosynthetic index as might be expected had home range size been closely adjusted to [the] supply of insect food. . . ." Later he points out, "that bird breeding territories, rather than being adjusted to food needs, are on the average in excess of them."

As indicated in figure 3 and discussed earlier, when food resources in a desert habitat were, by inference, low, *C. minor* altered the composition of its diet. Since this is a substitution for the "preferred" diet (flying ants), it seems reasonable to assume that the fitness of the species under these conditions would be adversely affected. During these periods, insect swarms and aggregates are less readily available, necessitating a more generalized feeding regime. *C. minor* cannot readily compensate for this decline in density of the most suitable food sources because of its strong territorial ties. Since the search area could not be increased without leaving the territory, *C. minor* seems to compensate for the low food density by utilizing less suitable food sources.

The flight characteristics of *C. minor* appear to be adaptations to the demands of defending large aerial territories. To defend territories of such large volumes in a medium with few physical markers or barriers, individuals have to be both very conspicuous and very mobile. Boundaries can be recognized only by their relatively frequent reassertion by the defending bird. Auditory conspicuousness is evident in the loud calls which can be heard from a considerable distance and also in the characteristic boom of this species (Miller 1925). The white wing bars may function in agonistic display as has been suggested for the wing-flashing of the Mockingbird (*Mimus polyglottos*) by Selander and Hunter (1960).

In order to deliver these auditory and visual signals at a rate sufficiently high to maintain territorial boundaries, a relatively rapid flight would be necessary. Concurrently, this flight mode would have to be energetically undemanding. In addition, on the very large territories of *C. minor*, the ability to rapidly approach an intruder from a distant territory margin would also be of great advantage. The

two distinct flight modes of *C. minor* would seem to fulfill these requirements. The alternation from the seemingly leisurely flight mode of territorial patrol to the very rapid flight of pursuit often was observed.

Imposed upon these needs for territorial defense are the demands of obtaining food and water while in flight. Maneuverability and control would be important for efficient aerial feeding. However, the higher flight speed and greater wing loading and aspect ratio of *C. minor* would provide for a considerably less maneuverable flight mode than that of *C. acutipennis*. This may restrict *C. minor's* ability to feed in close proximity to vegetation surfaces, as *C. acutipennis* often does.

COMPETITIVE INTERACTIONS

The evidence for competitive exclusion (Hardin 1960) in the form of habitat displacement of *C. minor* by *C. acutipennis* has come mainly from comparisons of habitat utilization in the allopatric and sympatric distributions. Hutchinson (1957) distinguishes between the fundamental niche and the realized niche. A decrease in the breadth of habitat utilization by one species as a result of competition from a second species is an example of the compression of the fundamental niche into a smaller more restricted realized niche. This kind of restriction of the fundamental niche through competitive interactions has often been cited as support for operation of competitive exclusion (Hutchinson 1957; Miller 1964, 1967; Heller 1971; Sheppard 1971; Brown 1971). Such restriction in habitat utilization was pointed out above for *C. minor* within the sympatric distribution, suggesting that competitive exclusion is operative.

There are only two environmental resources for which *C. minor* and *C. acutipennis* would seem likely to compete. These are food and space. The diets of both species were very similar through a major portion of this study (fig. 4), indicating that the food niches were similar. The question whether the food resource was actually or potentially limiting is more difficult to answer because data on insect density are lacking. The availability of food was estimated only indirectly.

There are two components of the competitive process: exploitation and interference (Elton and Miller 1954; Park 1954). Miller (1967:12) points out that both elements of competition are generally present in most competitive interactions. However, exploitation seems characteristic of simple metazoans

where social interactions are uncomplicated or lacking, while interference is well developed among the higher vertebrates. In order for exploitation to exert a significant influence on the competitive relationships of these nighthawks, *C. acutipennis* would have to remove sufficient amounts of food to alter significantly the density of flying insects. The likelihood of this occurring would seem low, except possibly on a very local and/or temporary basis.

Interference competition operates by limiting a competitor's access to a necessary resource or requirement. Under certain circumstances aggression can function as a form of interference competition, strongly influencing the competitive relationships. This can take place in two ways. The more aggressive species can be the source of interference competition through a direct subjugation of a subordinate species, thus preventing that species from utilizing various environmental resources; or, the more aggressive species may itself be placed at a disadvantage by devoting too much time and energy to aggressive behavior.

Since *C. minor* generally does most, if not all, feeding within a territory from which *C. acutipennis* and other *C. minor* are excluded, competition for food and space cannot be easily separated when considering the effects of interference. Because *C. minor* excludes *C. acutipennis* from its territories, this aggression can be considered a form of interference competition. *C. acutipennis* would be unable to use either the space or food resources being defended by *C. minor*. Notwithstanding this, *C. acutipennis* is competitively superior in desert habitats. Therefore, there must be some other factor mitigating against exclusion of *C. acutipennis* from desert habitats. One possibility is the phenomenon of aggressive neglect postulated by Ripley (1959). He described the interactions of *Nectarinia sericea* (Nectariniidae) and *Mysomela obscura* (Meliphagidae) on the northern Moluccan Island of Batjan. The more aggressive and dominant *M. obscura* was the scarcer species, but the territories of the species coincide. Ripley suggested that, in this situation, "aggressiveness may in itself serve to limit successful reproduction. . . ." This relationship he termed aggressive neglect. Hutchinson and MacArthur (1959) defined this aggressive neglect as, "the tendency of one species to neglect its brood, owing to the release of excessive aggressive behavior due to the presence of a second species." Ripley (1961)

later suggested other possible examples from natural populations of birds.

Definitive evidence for aggressive neglect would, of necessity, include documentation of a decreased reproductive rate within the area of overlap. In species such as these night-hawks, where nests are widely dispersed and difficult to locate, this direct evidence would be very difficult to obtain. However, certain indirect evidence is available. In areas of habitat overlap, *C. minor* was the more aggressive and dominant species. Also, *C. minor* defends larger territories than the subordinate species. *C. acutipennis* was regularly observed flying through *C. minor* territories and, when spotted by the resident bird, always seemed to elicit aggressive responses. Thus, the interactions of the nighthawks appear very similar to those described by Ripley for the sunbirds and honeyeaters and may be a form of aggressive neglect.

Aggression has been shown effective in maintaining contiguously allopatric distributions of chipmunks (*Eutamias*) by Brown (1971), Heller (1971), and Sheppard (1971). These situations are very similar to those presented in this study. In each case there is vertical stratification of the species in a mountain range. Aggression and habitat selection together determined and maintained the lines of contact between the competing species.

The chance of an interspecific encounter is directly related to the density of both species. In the areas of habitat overlap, the density of *C. acutipennis* declined from high densities on the desert lowlands to absence at the lower elevations of the adjacent mountains. Since each interspecific encounter on a *C. minor* territory seemed to produce an aggressive response, the total amount of aggression demonstrated by *C. minor* is related to the density of *C. acutipennis*. Thus the further into the desert habitats which *C. minor* establishes as territories, the greater the density of *C. acutipennis* and hence the greater the likelihood of aggression elicitation. The effective densities of *C. acutipennis* would result from factors related to both dispersion and changes in abundance resulting from local movements; i.e., the increased chances of territorial transgressions resulting from the close proximity of *C. minor* territories to preferred feeding areas of *C. acutipennis*. If there is a limit on the amount of time and energy which *C. minor* is able to devote to aggressive behavior, and, if *C. acutipennis* causes this limit to be exceeded, then aggressive neglect would be

influential in preventing co-occurrence of *C. minor* and *C. acutipennis* in desert habitats.

SUMMARY

Competitive relationships and mechanisms for the maintenance of habitat displacement were investigated in the Common and the Lesser Nighthawk by studying habitat distributions, behavioral interactions, flight mechanics, and food habits. A one-way habitat displacement seems to result from the exclusion of *C. minor* from desert habitats occupied by *C. acutipennis*. Specific adaptations contribute to the competitive superiority of *C. acutipennis* in desert habitats; these include lack of pronounced territoriality, a slow maneuverable flight pattern, little aggressiveness, and the propensity for wandering great distances in search of food and water. *C. minor* is highly territorial, is capable of two distinct flight modes, is highly aggressive, and generally feeds within territory boundaries. Analyses of stomach contents indicated much overlap between the species and similar levels of specialization; however, when, by inference, food became limiting, the diet of *C. minor* became increasingly generalized while diet overlap declined. Arguments are presented to show that *C. minor* is best adapted to conditions where food is seldom limiting, while *C. acutipennis* is adapted to conditions where food resources may often be of low density and/or highly dispersed. Evidence indicates that aggressiveness may act to prevent co-occurrence of the species in mutually suitable habitats. These aggressive interactions may function in the form of aggressive neglect. In areas of co-occurrence, the more aggressive and dominant *C. minor* spend a considerable amount of time excluding *C. acutipennis* from their territories. It is suggested that this time and energy are of sufficient magnitude to place *C. minor* at a competitive disadvantage in areas of co-occurrence with *C. acutipennis*.

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