

POPULATION REGULATION AND THE BLACK-CAPPED CHICKADEE
(PARUS ATRICAPPILLUS): A THEORETICAL DISCUSSION AND
AN APPLICATION OF THE THEORY OF ECOTYPIC SELECTION

by

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INTRODUCTION

Birds are favorite subjects for population regulation studies. In game bird species, information gained from such studies is often put to use in management programs supported by public money. Information gathered about songbird population regulation is usually not used for this purpose, but as the concept of management for all species becomes popular, I feel there will be place for application of songbird population regulation knowledge. One way to understand how to use population regulation in a management program for songbirds is to choose a species and study some aspect of its population regulation. Then one could make suggestions for management programs to increase the numbers of that species.

I decided to apply this strategy to the Black-capped Chickadee (Parus atricapillus). Since this bird is easily attracted to feeders and nestboxes and can be approached closely most of the year, its natural history has been well documented. The Black-capped Chickadee is also a likely candidate for management efforts. It is a favorite with bird enthusiasts, especially those who feed birds in the winter. In addition, the species may control certain insect populations on which it feeds. Thus, the Black-capped Chickadee is a popular and possibly economically important species, and a study of its population regulation is likely to generate information that could be put to use in increasing chickadee numbers.

My first step in the population regulation study was a thorough survey of the literature available on the Black-capped Chickadee. The results are described below as an annual cycle starting in early spring. Most of the available literature was natural history information, rather than population regulation information, so I tentatively suggested the way several theories of population regulation might apply to the natural history literature. These applications are interspersed throughout the description of the annual cycle, to suggest which theories would be suitable for further application.

The theory that appeared to be most suitable for more detailed application by me was the theory of ecotypic selection. This theory would answer questions about the relationship of chickadees with competitors, and the effect competitors have on chickadee numbers. Also, I would be able to use museum specimens to investigate this theory in one year, where investigations of the other theories would have taken several years of field work that I would not have time to complete.

The ecotypic selection theory deals with niche width of species and individuals, and predicts the situation where species will directly compete because of overlapping resource bases. I present this theory in detail in a separate section, which begins with a history and explanation of the theory of ecotypic selection. The theory and the use of morphological measurements in testing this theory is verified in groups of hawks whose niche widths and feeding strategies have been well studied through extensive field work. Finally, the theory is applied to the winter woodland insect-eating

community, of which the chickadee is a part. Importance of competing species is evaluated, and some ideas for management are suggested.

SECTION I

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LIFE HISTORY
OF THE BLACK-CAPPED CHICKADEE

Range

The Black-capped Chickadee ranges through much of the forest and woodland of northern North America. The American Ornithologist's Union Checklist (1957) describes its range as extending from central Alaska, southern Yukon, southwestern Mackenzie, central Saskatchewan, central Manitoba, central Ontario, southern Quebec, and Newfoundland, south to northwestern California, northeastern Nevada, central Missouri, south-central Illinois, central Indiana, southern Ohio, West Virginia, western Virginia, eastern Tennessee, western North Carolina, western Maryland, Pennsylvania, and northern New Jersey. The Black-capped Chickadee is replaced in the south by the similar Carolina Chickadee (Parus carolinensis).

Apparently, Black-capped Chickadees are not limited to deciduous forest, since much of this described range is coniferous. This lack of limitation implies a versatility in food habits, since the insects in a conifer forest are different from those in a deciduous forest. Their range extends further north than that of many insect eaters, and only in the hardest winters are they forced to vacate the northern reaches of their range (Wallace, 1941).

A theory which can be applied here deals with the range of species (MacArthur, 1961), and says that nesting success increases to the north due to decreased competition. However, death rate also increases at a faster rate due to climatic extremes. At some latitude the rising death rate becomes greater than the birth rate,

which has stabilized as competition becomes unimportant. The northern limit of the range occurs at this point. The limit of the southern range is reached when the birth rate, decreasing with decreasing latitude because of increasing competition, goes below the death rate which is decreasing only slowly as climate becomes unimportant in limiting the population. Detailed investigation of this theory would require a study of the complex factors that cause birth rates and death rates to be what they are, such as predation and food availability.

Below, I will relate this theory to clutch size in different parts of the range. This will suggest an explanation for the limit of the southern edge of the range.

An interesting fact about the southern edge of the range of the Black-capped Chickadee is that there is a buffer zone between it and the northern edge of the Carolina Chickadee range. This buffer zone is about thirty miles wide, is found in most places where the ranges approach each other, and contains essentially no chickadees of either species (Brewer, 1961). Brewer felt this was an evolutionary adaptation to the low fitness of hybrids between the two species. Since the two species are so similar, it could also be an adaptation to reduce competition. This possibility supports the investigation of competition by the application of the theory of ecotypic selection, since it suggests that competition could be important in chickadee population regulation.

Preliminaries to the Breeding Season

Flock Breakup and Pairing. The winter flocks of chickadees become unstable in March, and the birds change flocks or roam alone more frequently than in winter. Later in March and in early April the flocks break up for the season. This breakup is gradual, with pairs and individuals separating out a few at a time.

After flock breakup, the birds pair. Most birds pair in April or May with their mate of the previous season if that mate is still alive (Lawrence, 1958; Odum, 1941a). Courtship is brief and uncomplicated, lasting about four days and having no obvious ritual (Odum, 1941a). Wing-fluttering ceremonies, the "fee-bee" song of the male, and a special twittering mating note may help gradually strengthen the pair bond, however.

Spring Population Decline. Odum (1941a) and Smith (1967) gave evidence that much of the winter population leaves, or is forced off, the winter range in early spring. Odum found that no more than two pairs of birds remained on the winter range at this time. Since the average flock size in his study was seven, at least a little less than half the flock left the winter range. Smith, studying birds in what she considered an optimum habitat, found that many birds moved out of her study area at this time of year and were not replaced by ones coming in from other areas. Since this population existed in a time of apparently plentiful food, and since most of the birds which left were not seen again, Smith felt this decline

was an example of behavioral regulation of a population in anticipation of an environmental limit occurring either later in the breeding season or in the winter.

A theory of population regulation by territorial behavior (Fretwell, 1972) can be applied here. Although the chickadees have not established territories yet, the population has been spaced out by a behavioral mechanism, so application of the theory is valid.

In this theory, there are two options for a dispersal mechanism in a species. In the first option, a bird trying to establish a territory sees optimum, but crowded, habitat as less attractive than suboptimum, but uncrowded, habitat. Birds will go to the suboptimum habitat until it too is crowded, and then they will go to a third habitat. In this situation, already established birds do not force unestablished birds out by aggressive action, but simply advertise their presence by singing and conspicuous behavior. Population levels can be increased by improving and creating more of the suboptimal habitats.

In the second option, unestablished birds are actually forced out by physical aggression from established birds. Birds can be forced into habitats where their birth rate is lower than their death rate. Population levels can only be increased in this situation by creating more of the optimum habitat.

In a tentative application of this theory to chickadee populations, several factors must be considered. First, there is the evidence of Kluyver and Tinbergen (1953) indicating that the first system is operating in European titmice. Odum (1941a) and Smith

(1967) give evidence that the second system is operating in Black-capped Chickadees. However, Odum found that it is dominant birds that stay on the winter range, indicating that the winter range is optimum habitat and that subdominants are probably forced off by the aggression of the dominants. Since Smith found that most of the birds which left the winter range never reappeared and were not replaced by birds coming in from other ranges, it appears that the birds forced off the winter range may have died. Her evidence indicates that death rate is high in certain habitats. The more frequent singing by males during this time than after subdominants are driven off the winter range (Dixon and Stefanski, 1963) and the frequent fighting between males at this time (Bent, 1946) are other indications that subdominants are forced out by aggressive action.

It seems likely, therefore, that the second system is operating in chickadee populations. This idea could be tested in depth by looking at death and birth rates in different habitats, and by observing birds on the winter range in early spring. If the idea were confirmed, then chickadee numbers could be increased by increasing the winter range type of habitat.

Territories. Territorial behavior probably does not cause the dispersion of chickadees as much as preterritorial behavior does. Evidence for this idea is that males do not sing or fight as frequently after territories are established as before, and subdominants have already left the winter range by the time territories are established.

However, territories are actively defended, and therefore

probably function in maintaining the dispersal brought about by pre-territorial behavior. Chickadee males defend territories with vocal duels, but little or no visual display (Odum, 1941a). The song is a whistled "fee-bee" or "fee-bee-bee" with the first note more drawn out and higher than the second one (Bent, 1946; Forbush, 1929; Forbush and May, 1939; Gross, 1891; Roberts, 1932; Rokker, 1889; Warren, 1890). Singing is done primarily by the male, but occasionally, when the male and female defend as a pair against another pair, the female will sing (Bent, 1946). If aggression becomes intense, males will fight and fall to the ground (Odum, 1941a).

Territory sizes vary, but all seem to contain about the same amount of suitable habitat. In one study (Odum, 1941a), chickadee territories in mixed deciduous woods in New York ranged from 8.4 to 17.1 acres, and averaged 13.2 acres. The larger territories contained more unsuitable field-type habitat than the smaller ones.

There are two types of habitat necessary in chickadee breeding territories, one type for nesting and one type for feeding (Odum, 1941a). The feeding habitat is a late seral vegetation stage (beech-hickory forest, for example), and the nesting habitat is an earlier seral stage of birch, willow, and other soft-wooded or young trees. These soft woods are probably necessary for the chickadee nesting site of an excavated branch stub.

Limitation by Food. Chickadee populations are probably not limited by food at this time of year. Betts (1955) found that European titmice eat less than five per cent of the available insect food during spring and summer. Food habit studies of the

Black-capped Chickadee in this country showed that chickadees increase their consumption of preferred animal food from 70.7% in winter to 100% in summer (Sanderson, 1898), suggesting that they can find all the food they need.

Conclusion. Dispersal in early spring probably has an important role in the population regulation of the chickadee, and may be maintained by territorial behavior. Chickadee populations are probably not limited by food at this time of year.

The Breeding Season

Nest Sites. After the territory is established, the pair begin to select a nest site. The favorite nest site of chickadees is a soft, partially rotted branch stub that they can excavate themselves (Barrows, 1912; Bent, 1946; Forbush, 1929; Forbush and May, 1939; Gross, 1891; Odum, 1941b; Roberts, 1932; Rokker, 1889; Warren, 1890). In fact, this urge to excavate is so strong that chickadees will rarely use nest boxes unless the boxes have been filled with a mixture of peat moss and sawdust so they can be excavated (Drury, 1958).

Chickadees usually use soft wooded trees for nesting, so they can excavate their own hole, but they occasionally nest in old woodpecker holes in hard-wooded trees (Barrows, 1912; Bent, 1946; Forbush, 1929; Forbush and May, 1939; Gross, 1891; Odum, 1941b; Roberts, 1932; Rokker, 1889; Warren, 1890). Bent (1946) reported the most common nest-hole tree in the northeast United States was the gray birch. In Kansas, Black-capped Chickadees commonly excavate holes in willows, elms, cottonwoods, and honey locusts (Johnston, 1964).

Male and female cooperate in excavation, as they do with other tasks of the breeding season, by taking turns throughout the day for seven to ten days (Bent, 1946; Forbush, 1929; Forbush and May, 1939). This cooperation is not seen in pairs where the male is a Carolina-Black-capped hybrid. Hybrid males do not excavate at all (Brewer, 1961).

After the cavity has been excavated both sexes again cooperate in gathering nest materials. The female constructs the nest (Bent, 1946; Odum, 1941b), and it is made of moss overlaid with fine bark strips and lined with fur.

The nest site is inconspicuous, both because of its resemblance to a mere rotten branch, and because the chickadee pair carry all the chips from excavation well away from the nest site (Odum, 1941b). These are probably adaptations which decrease nest predation.

However, the height and depth of the cavity do not appear to make it particularly predator resistant, since the cavity is often low and the opening large. In one study, nest height varied from two to 30 feet, but the average was four to eight feet (Bent, 1946). In another, heights were from four to 20 feet, averaging ten feet. Depths of the cavity range from five to 6.25 inches, and the stub itself was usually 2.5 to 2.745 inches in diameter. The entrance hole at the end of the stub is an average of 2.25 inches in diameter (Bent, 1946).

Since studies have shown that the Great Tit (Parus major) is limited by nesting sites (Kluyver, 1951), it is reasonable to ask if the Black-capped Chickadee is also. Since the Great Tit does not construct its nest hole but must rely on existing ones, availability of nest holes could be a limiting resource. The Black-capped Chickadee, unlike the Great Tit, utilizes a second habitat, in addition to his feeding habitat, strictly for constructing a nest hole. Since chickadees can move into a second habitat and construct their own nest holes, it is less likely that this would be a limiting resource.

More evidence that nest holes are not limiting is that a chickadee pair may excavate several branch stubs before finally settling on one. This suggests that the right kind of branch stub is numerous enough in the chickadee nesting habitat to make it difficult to choose between several. Also, nest holes are usually not used a second year, indicating that appropriate branch stubs are readily available.

Replacement of Mates. Chickadees sometimes lose mates during the breeding season, but lost mates are usually quickly replaced (Odum, 1941b). Butts (1931) reported a female who had three mates in one season, each one taking up raising the brood where the last one had left off.

This quick replacement of mates could indicate the presence of a breeding surplus of birds off the breeding grounds. These replacement birds could be birds previously driven off by dominants, but able to return when death creates an opening. If this is true, then Butts' report shows it is important enough for a bird to get out of the breeding surplus that a male will raise young that are not his.

Survival may be one reason it is important for a bird to get out of the breeding surplus. Smith (1967) felt that most of the birds forced off the breeding grounds probably died, but Odum (1942) found that the survival of adults not forced off the breeding ground is high, about 90%. Evidence that clouds this idea, however, is that one female lost her mate before her eggs hatched, and he was not replaced. This indicates that either there is no breeding surplus, or that the breeding surplus is far away or dead by the time

the breeding birds are nesting.

Egg-Laying and Clutch Size. After the nest is constructed, the female begins roosting in the cavity and laying eggs (Odum, 1941b). The female lays one egg a day in the morning until the clutch is complete (Bent, 1946), and the pair spends the rest of the day feeding and resting, often out of sight of each other. At dusk the male escorts the female to the cavity, and then he may delay as much as half an hour before going to roost nearby.

About the start of egg-laying, the female begins a wing-fluttering, crouching display that stimulates the male to bring her food. This display is strongest at the start of egg-laying, when the pair have relatively few chores, and is phased out as they become busy with feeding young. Displays of this type may strengthen pair bonds so this may indicate that egg-laying and roosting in the cavity are not as effective in strengthening the pair bond as feeding the young.

A clutch of seven eggs is average (Bent, 1946; Brewer, 1961; Odum, 1941b) but it ranges from five to ten (Forbush, 1929). The clutch is larger in northern latitudes (Brewer, 1961), and smaller later in the breeding season.

A theory of clutch size of passerines (Fretwell, ms.) can be applied here which relates breeding success to clutch size by a factor of ten. In other words, large clutches indicate high nesting success, and small ones, low. According to this theory, birds in northern latitudes should have higher rates of nesting success than those in southern latitudes, and birds nesting early in the season,

higher than those nesting later. Also, the average nesting success should be about seventy per cent.

Some of the data in the literature tends to support these predictions. Smith (1962) and Odum (1941b) report that second broods are only rarely attempted, even when the first one is destroyed before maturity. More supporting evidence is the fact that as the season progresses parents become more protective of their brood, suggesting that they would be less able to raise a second brood later in the season.

In the case of the prediction of higher nesting success in northern latitudes, the literature does not directly confirm the prediction but it provides material for an interesting hypothesis about the ranges of the Black-capped and Carolina Chickadees. At the same latitude, the Carolina Chickadee lays a larger clutch than the Black-capped Chickadee. The clutch size theory would predict a higher nesting success for the Carolina Chickadee at a given latitude. This leads to the hypothesis that the Carolina Chickadee is able to extend its range further south than the Black-capped Chickadee because of its higher nesting success at southern latitudes.

The clutch is large for such a small bird, especially compared to the clutch size of small, open nesting birds, and indicates a high population turnover sometime during the year. Both the evidence of Odum (1942) and Wallace (1941) that adult resident birds have high survival rates in summer and winter and the evidence of Smith (1967) and Odum (1941a) that subdominant birds are forced off the breeding grounds and are not seen again point to the conclusion that

this turnover occurs in early spring.

Incubation and Care of the Young. The male chickadee does not incubate (Bent, 1946; Odum, 1941b; Wallace, 1941), but he is kept busy by feeding the female. Odum (1941b) reports that the male appeared at the mouth of the cavity to feed the female at intervals averaging 25 minutes. He would utter a soft "seep" note to announce his approach. She usually left the nest for a rest period of about ten minutes, and the male continued to feed her during this rest period.

An indication that nest predation is, or was in the evolutionary history of the chickadee, a factor at this time is the hissing snake display given by the incubating female when disturbed. She will rear back, then dart forward with an explosive hiss, often hitting her wings against the walls of the cavity (Sibley, 1955). This display is very similar to the display of a copperhead snake disturbed while resting in a rotten stump, undoubtedly having a frightening effect on any would be predator.

After an incubation period of twelve or thirteen days, the young hatch (Bent, 1946; Allen, 1929; Odum, 1941b) and the female broods the young for a week. The female feeds the young while she broods, but only about one-fourth to half as often as the male (Kluyver, 1961).

After the young hatch, the formalities of displays and mating notes begin to give way to the demanding task of feeding the young. The female no longer gives a begging display when fed by the male, and the male doesn't utter the "seep" note on approaching the nest.

The rate of weight increase of a nesting bird and the number of times it is fed in a day gives an idea of how demanding the task of feeding young is. Odum (1941b) reported a rate of weight increase for nestlings of nine grams in twelve days. This means that the parents must provide, for an average clutch of seven, enough food for 5.25 grams of growth per day. Kluyver (1961) observed 21 to 29 feedings per day per young during the first days after hatching, and this later increased to 30 to 36 feedings per day per young. Lepidoptera larvae were the primary food for nestlings, with spiders second, and parents would change feeding areas to follow the caterpillar supply.

Fledging and Fall Dispersal. Young are fledged sixteen or seventeen days after hatching (Odum, 1941b), and they stay with their parents for about a month after fledging (Brewer, 1961; Kluyver, 1961). The parents feed the young for this month, but do not defend their territory.

After leaving the parents, the young group together in irregular, unstable flocks and may travel considerable distances (Lawrence, 1958). When the young on Smith's (1967) plot dispersed, they were replaced by young evidently fledged on other plots.

This fall dispersal of young could be a time when the Black-capped Chickadee population is regulated. However, the mortality of dispersing young is not known. The population of chickadees on Smith's (1967) plot did not decline at this time, and she felt there was low mortality for dispersing young. Odum (1941b) believes that early fall is a care-free time for chickadees, when adults have

plenty of food but no young to feed, and the young are able to wander, free from food or predator worries, until they find a place to spend the winter. However, Drury (1958) says this time is one of high mortality of young for most species. And Lack (1966) felt that the Great Tit populations are regulated by high fall mortality.

Adults and young may migrate down from northern ranges at this time of year, probably in response to low levels of food. Butts (1931) saw a southward migration at this time. Lawrence (1958) reported chickadees in her area had migrated south from Pimsi Bay, Ontario, after a cold and sunless summer. She felt the weather had caused a low insect crop, and the chickadees were migrating in response to this.

Food as a Limit in the Breeding Season. Most reports indicate that food is not a limiting factor during the breeding season. Food is probably plentiful, since parents rarely have to go further than fifty yards from the nest in their search for the large amounts of food needed by nestlings (Bent, 1946). Also, chickadees are able to find enough insects, which they prefer over seeds, to make up 100 per cent of their diet (Sanderson, 1898).

Limiting resources are often defended by territorial behavior, so the fact that territories are not defended at all after the young fledge when they need more food than ever, suggests that food may not be limiting (Odum, 1941b). However, defense of food simply may not be a function of the chickadee territory.

Conclusion. Most evidence points to the conclusion that chickadee populations are not limited at this time of year. Survival of

adults and young is fairly high, and most indications are that food is abundant.

Wintering

Flocking. Chickadees winter in flocks of variable size. Some average flock sizes given in the literature were twelve (Butts, 1931), three to four (Brewer, 1961), "several" to six or eight (Wallace, 1941), seven to eight (Odum, 1942), and three to four (Robbins and Rain, 1970). Flocks of four seem to be most common in a woodland area in Kansas (pers. obsv.).

However, the most striking aspect of chickadee flocks is not their size, but their variability. Flocks may change from day to day and hour to hour (Odum, 1942). Two flocks may meet, merge, and then split into two flocks different from the original two. The flocks are loosely organized, seeming to be a balance between the chickadee's essentially independent nature and the desire to flock. The flock movements are not directed by any one bird; instead, it appears the flock is directed by each bird trying to go his way and get the rest of the flock to follow him. The final direction is an average of all the birds' wishes.

Odum (1942) studied flock movement and found it was rhythmic, rather than uniform, and varied with time of day, time of year, and weather. The flocks he observed moved faster in the morning than in the middle of the day, faster in October than in any other month, and faster on warm cloudy days than on cold, windy days. I attempted to mentally evaluate these rates of movement with respect to the difficulty of finding food, but results were not conclusive.

Winter flocks have dominance hierarchies, but the hierarchal order is obvious only in the vicinity of a feeding station (Hammerstrom, 1942; Odum, 1942). However, the orders are not linear or fixed. Males are usually dominant to females, and residents to newcomers.

Hierarchy position does not determine winter survival, but may play an important role in mating and breeding success (Odum, 1942). Subdominants eat as much as dominants (Hammerstrom, 1942), so apparently the hierarchal system is not built around the food resource.

Function of Flocking. A relevant question that can be asked here is, what is the function of flocking and what is the relationship of this function to the population regulation of the chickadee? In many species, flocks function in protection from predation. This function implies that predation is, or was, in the evolutionary history of the chickadee, an important factor in the population regulation of the species.

One indication that protection from predators may be a function of the flock is the use of contact notes and warning calls by members of a flock. One note in particular is a long, high pitched waver used to warn of avian predators (Odum, 1942). The peculiar frequency and low volume of this note makes its source hard to locate. This warning note seems to work, since chickadees are rarely found in the stomachs of avian predators (Wallace, 1941).

Another indication that predator protection may be a flock function is the way other species, especially transient kinglets, warblers and vireos, flock with chickadees and heed their warning

notes (Odum, 1942). Forbush (1929) described a situation where a flock of migratory warblers, having arrived the previous night, spent the morning in their own flock, uttering their own warning and contact notes. By afternoon they had joined with a chickadee flock and were silent, but were responding to chickadee contact and alarm notes. Forbush felt that the migratory birds had actively sought the resident chickadee flock, because the chickadees were more familiar with both the predators and the choicest feeding areas of a region.

Other birds who associate with chickadee flocks, and thereby have some extra eyes to watch for predators, are White-breasted Nuthatches (Sitta carolinensis), Red-breasted Nuthatches (Sitta canadensis), Golden-crowned Kinglets (Regulus satrapa), Brown Creepers (Certhia familiaris), and various kinds of woodpeckers (Odum, 1942). Most of these birds were not closely attached to the chickadee flock, however.

The effect of flocking may be to reduce predation so that it is not a factor in the population regulation of the chickadee. Winter mortality is 10-20% (Wallace, 1941) so even if all these birds were lost to predators, winter predation is still not as important as the spring decline seen by Smith (1967).

Winter Feeding. Winter flocks do all their feeding within flock ranges. These ranges often overlap, and the chickadees do not defend them (Odum, 1942).

Some sizes given for these ranges were 21 to 55 acres, with an average of 36 acres (Odum, 1942) and 5.2 to 80.3 acres, with an

average of 31.4 acres (Robbins and Rain, 1970). Larger ranges contain more open ground than small ranges, so the amount of feeding habitat in all ranges is similar (Odum, 1942). This implies that there is a certain fairly large acreage of minimum feeding habitat needed by a chickadee flock, and that winter food may be limiting.

The winter food of the chickadee is primarily insects, but in certain months the percentage of insect food in chickadee diets drops below the percentage of vegetable food. Since insect food is preferred by chickadees (Davison, 1967), the month when insect food is hardest to find can be determined by seeing which month insect food is at its lowest level in chickadee diets. This will not necessarily mean that this is the month when chickadee populations are regulated, since insect food has not been shown to be limiting.

One study found the amount of insect food to be at a low of 16% in January (Weed, 1898). In this same study, chickadee diets were 80% insects in November and December, and 50% in February and March. The increase from 16% to 50% from January to February means that insects were much harder to find in January than in February, or that, improbably, the insects reproduced in January. Although Murton (1971) feels that insects do reproduce some in winter in England, it seems more likely that cold January weather may have reduced insect movement so that the insects were more difficult to find. Lepidoptera larvae, which may not move in cold or cool weather, were taken in February and March, but not in January, suggesting this is a reasonable explanation.

Insect eggs stay in the same place throughout the winter months

and are a staple item in the chickadee winter diet. Almost all of the 16% insect matter in the diet of chickadees in Weed's (1898) study were aphid eggs. This percentage is not far from the percentages eaten in other months.

In my own examination of bark and twigs for possible insect food, I was able to find insect eggs easily. Larvae and pupae were much harder to find. I found 4.7 eggs per square inch on the branches of bitternut hickory, but only 0.08 items of any other kind per square inch.

If chickadee populations are limited by winter food, then a "crunch" period could be caused by a cold snap which makes insect food hard to find. Insect eggs could soften this crunch somewhat since they seem to be equally available throughout the winter.

A factor that could make this crunch period more severe, however, is interspecific competition. In most of the Black-capped Chickadee range there are several other species of birds which glean insects and insect eggs from bark. Some examples are the Golden Crown Kinglet and the Tufted Titmouse.

Interspecific competition can only occur when species in an ecological community are feeding on resource types which grade continuously in size and are all equally available. Application of the theory of ecotypic selection can determine if resources are continuous, and therefore if competition is a factor in chickadee population regulation in winter.

Artificial Feeding. One way to evaluate the importance of the winter food resource in population regulation of chickadees is to

investigate the effect of winter feeding on a population. If feeding can bring about a population increase in one winter season, then this would be good evidence for winter food limiting a chickadee population. However, if it does not ever bring about an increase, or if the increase takes several years, then this is an indication that either other things, like behavioral regulation and competition with a species that is also benefitted by the feeding, are going on, or that winter food is not limiting. Behavioral regulation, if it were a genetic adaptation to low winter food, could take several to very many years to be re-set at a higher level. Competition with another species which also benefits by the feeding could slow the population increase of both species, since a slight increase in one caused by artificial feeding could depress part of the natural resources of the other, if they share some resources. The theory of ecotypic selection will be applied below to determine if they are sharing resources.

Odum (1942) found that birds were more concentrated in the area of a feeding station and that the average flock was larger (twelve as compared to seven away from the feeder). Wallace (1941) found that a feeder will cause some flocks to extend their ranges to include the feeding station. Since flock ranges overlap without aggression and defense of range, it can be seen that if several winter flocks extended their ranges so that they overlapped at a feeding station and the flocks spent much time at the feeder, the result would be a concentration as described by Odum, without any real population increase. Hammerstrom (1942) supported this conclusion,

reporting that feeding stations do not cause any real population increase, except possibly after several years. This evidence indicates that chickadee populations are not limited simply by the winter food supply. Either they are not limited at all by winter food, or some of the other things mentioned above are going on.

Roosting Sites. Another factor in the population regulation of chickadees may be the availability of good roosting sites. Chickadees will usually roost in cavities if they are available, according to the Tennessee Ornithological Society (1943). If roosting in cavities is important to winter survival, then the population might be limited by the number of cavities meeting the needs of chickadees. All members of a population studied by Odum (1942), however, did not roost in cavities even though they were available. Instead, most birds roosted as flocks in conifer stands. This suggests that other things, such as being in a flock, may be more important than roosting in cavities.

Winter Movements. There is some evidence for winter movement of chickadees out of the northern reaches of their range in extra cold winter, indicating that at very cold temperatures, either winter food or, less plausibly, roosting sites become limiting. Lawrence (1958) saw a peak of new birds on her study area in southern Canada in the fall, a second peak in January, and a third in March during a cold winter in Canada. She felt these new birds may have come down from northern Canada. Wallace (1941) gave evidence for withdrawal from northern regions and influx into southern ones during particularly harsh winters.

Conclusion. There is conflicting evidence of the importance of

the winter food supply in chickadee population regulation. Roosting sites may be limiting, but there is some evidence against this. Competition could also be a factor.

Summary

The Black-capped Chickadee ranges over much of the northern half of North America, even into Canada and Alaska. Chickadee habitat is forest for feeding, and younger woods or an earlier seral stage for nesting. Their ability to excavate their own nest holes may be an adaptation to reduce competition for nesting sites, and may mean they are not limited by nesting sites.

Winter flocks break up in late March and early April. Pairs form and male aggression is seen, but territories are not yet formed. Subdominants are forced off the winter range, and in one study this resulted in a population reduction until the young were fledged. The possibility of behavioral population regulation at this time is raised. A theory is discussed which shows that, if a breeding surplus is created by aggressive action of dominant birds, chickadee population could be increased by increasing the breeding ground habitat. Territories are established after pairing, and may serve to keep the breeding surplus off the breeding grounds.

Mated pair members cooperate in most breeding tasks. However, only the female incubates and broods. The average clutch size is seven, and the eggs take 12 to 13 days to hatch. A clutch size theory is discussed which predicts a nesting success of 70 per cent, which is confirmed by results in the literature. Reasons are given for the belief that nesting success decreases as the breeding season progresses, but the reasons for this are not known. Food does not

seem to be short at this time.

Young stay in the nest for 16 to 17 days, and then stay with the parents an additional 10 to 25 days, when the parents continue to feed them. Then during August and early fall the young group in unstable flocks and leave the area where they were fledged. Evidence for and against heavy mortality at this time is discussed.

Chickadees winter in loosely organized feeding flocks. A possible function of these flocks is protection against predators. Flocks have undefended, overlapping ranges which include a certain minimum of feeding habitat. The role of the winter food resource in limiting chickadee populations is discussed, and evidence is given for and against its playing an important role. Roosting sites as a limiting factor is also discussed, as is competition.

There is evidence for southward migrations of chickadees during extra cold winters.

The literature on the Black-capped Chickadee gives a picture of a population adapted to its fluctuating environment through high birth and death rates. However, no clear evidence of seasonal limitation was given, and the picture is clouded by the possibility of behavioral regulation. Competition with other species may be important, so this will be investigated in the next section.

SECTION II

ECOTYPIC SELECTION IN WINTER INSECT-EATERS

A History and a Confirmation

The natural history review pointed out many possibilities for study of chickadee population regulation. Investigation of most of these, however, would have required several seasons of field work. Even a simple study of winter food limitation would have required several winters of artificial feeding. An investigation of the existence of a breeding surplus in early spring would have required a long, extensive study involving a wide area and lots of banding. One aspect of chickadee population regulation that can be investigated in one year, however, is that of interspecific competition as revealed by application of the theory of ecotypic selection.

The theory draws on past theories for much of its content, so it can best be understood in the context of its historical development.

A traditional selection theory is the theory of archetypic selection. This theory describes several ways selection can operate, but implicit in all these ways is the assumption that there is only one optimum phenotype for a population, and all other phenotypes have a lowered fitness. Since population members varying from the optimum have a lowered fitness, then this theory predicts that populations with large numbers of individuals with phenotypes varying from the optimum will have a lower overall fitness and a higher genetic load compared to less variable populations. In this theory, highly variable populations are thought to be the result of an

unpredictable environment, where the optimum phenotype changes from year to year (Soule, 1972). This theory does not explain all variation, however, because high variation is seen in populations in predictable environments, with no evidence of a higher genetic load than that of less variable populations.

A mechanism by which high morphological variation can be maintained in an experimental population was demonstrated by Thoday (1958). He showed that nonsexual polymorphism can be maintained indefinitely in a population under the condition of disruptive selection and positive assortative mating, where like mates with like.

The next step in the development of the theory of ecotypic selection was the demonstration of the advantage high variation could give to a natural population. Van Valen (1965) sought an example of an advantage when he showed that variation in a population could be adaptive when the species exploited a widened niche. He assumed that species living on islands would have wider niches than continental counterparts because of a lack of competitors, and he then demonstrated a higher continuous morphological variation for island species with many habitats to select from as compared to their continental counterparts with fewer habitats to select from. The idea behind this was, when the total species niche expands on an island, more individual niches within a species niche are available, and these different niches are best utilized by different variants, which can be called ecotypes, of the same species.

The same thing may be true on the mainland, but the amount of variation is not as great, since the number of individual niches

within the narrow continental niche is lower. This type of variation can be called ecotypic variation.

Another study which produced results similar to Van Valen's was that of Selander (1966). He was able to demonstrate a higher polymorphism of body size for an island woodpecker species than for a closely related continental species. He also demonstrated a greater difference in food habits and foraging locations and methods between the sexes of the island species than between the continental species. Selander felt that this was an example of a wider niche being exploited by a more variable species.

Carson (1961) demonstrated experimentally the advantage of genetic variation in a population of *Drosophila*. Out of three populations, one which was not irradiated at all, one which was dosed with an intermediate amount of radiation, and one which was dosed with a high amount, the intermediate one showed the greatest population increase in the experimental environment. These results were interpreted as showing that populations with an intermediate amount of variable genes, caused by radiation, were most successful in exploiting all the niches of their environment, and therefore could increase their numbers.

At this point in the history of the theory of ecotypic selection, then, a mechanism for the maintenance of variation in an experimental population had been found, and an adaptive reason for its existence in natural populations had been shown. However, the selective mechanism for the maintenance of variation in a natural population had not yet been demonstrated. Fretwell (1969) attempted to

remedy this when he presented field observations and a theoretical model that explained ecotypic variation with a theory of ecotypic selection. This theory provides a mechanism for the selection of ecotypes. His model employed density dependent fitness to show that for two phenotypes and two habitats, a stable polymorphism could be maintained when the phenotypes selected the habitat for which they were best adapted. His field observations showed that sparrows best adapted to certain habitats tended to spend more time in those habitats. The implications of this are that different phenotypes can all have equal or nearly equal fitnesses if the phenotypes select the habitat they are best adapted to. Roughgarden (1972) developed a complex mathematical model formalizing these concepts. His model shows that there is an optimum distribution for a given set of resources and regime of interphenotype competition.

Evidence that not all species with wide niches exploited their niches through different phenotypes exploiting subniches came when Soule and Stewart (1970) reported that the species they studied having wide niches were no more variable than species having narrow niches. Rothstein (1973) pointed out that they did not differentiate between the situation where all members of a population use the same wide range of resources and a situation where each member uses a different narrow resource range, causing the range of resources used by the entire population to be wide. Rothstein then goes on to report results which further support the theory that a diversity of phenotypes is adaptive in some situations.

This idea, that there are situations where the niches of

individuals are as wide as the whole species niche and other situations where individual niches are narrower than the species niche, is expanded on by Fretwell (ms.) and the different situations are related to feeding strategy and type of resources used by the species. This is the theory of ecotypic selection which I will later apply to the community of which the chickadee is a part.

A concept that must be understood before the final development of the theory of ecotypic selection can be understood is that of specialist versus generalist feeding strategies, described by MacArthur and Pianka (1966). In their model, individuals who put most of their food-getting energy into pursuing and catching their prey find it advantageous to specialize, since the prey item must be valuable and exactly what they want in order to repay them for the energy spent pursuing it. On the other hand, animals who spend a lot of time searching for their prey will be generalists, since they can't tell what they will find before they find it and must search for all prey items at once. Also in this paper is a comparison of consumers of dense resources versus consumers of sparse resources. Consumers of sparse resources are forced into the position of being searcher-generalists, since the amount of time they spend getting from one resource to the next forces them to take what is there when they get to it, and precludes spending very much time in pursuing it. On the other hand, consumers of dense resources, themselves dense unless they are predator limited, do not have to travel far between resource items and therefore can spend more time in pursuit. Also, their array of choices within a short search distance is

greater, so they can pick and specialize.

Fretwell's model (ms.) finally relates all this (feeding strategies, species niche width, individual niche width) to the type of resource base utilized by a community. According to his model, a situation where an individual's niche is as wide as his species' niche occurs when there are several similar competing species dependent on a continuous resource base where resources grade continuously and one size is no more numerous than any other size. In this situation, there is a tendency toward strong overlap of resource use between species. Resources of a size intermediate to those sizes preferred by each of two similar competing species are just as numerous as those preferred by just one of these species. This invites invasion from an intermediate species, unless the competing species are so similar that they competitively crowd each other and overutilize some intermediate resources. This might continue until all intermediate-sized resources are overutilized by being fed on by two adjacent species. When this happens, the species niche will be as narrow, and identical to, the niche of one individual.

Another situation where one individual's niche is the same as his species niche will occur when the species is dependent on discrete resources and is composed of generalist individuals. Discrete resources do not grade continuously in size, but are arranged into humps and troughs, where humps represent a resource abundant enough to support a species. In this argument, it is assumed that no more than one species will be using a resource hump and no species will use more than one hump. Troughs prevent invasion by intermediate

species, and so there is little competitive overlap. Therefore, a species niche does not have to be narrow. Species niche width is eventually constrained by the troughs on either side of a resource hump. For a species of generalist individuals, the niche of an individual can be as wide as the resource hump, which is the species niche. In this case, every individual uses all of the species niche.

A species niche can, however, be wider than the niche of individuals in that species if the individuals are specialists and the species is feeding on discrete resources. If a species is composed of specialist individuals, each individual will have a narrow niche. If they are feeding on discrete resources, the species niche will not be compressed down to the size of these narrow individual niches, so individuals of the same species can have niches different from each other and still be within a species niche. This leads to evolution of ecotypic variation, and a species composed of specialists will exhibit higher morphological variation than either a species of generalists or a species on discrete resources.

A testable prediction arising from this theory is that, if the species in question are feeding on discrete resources (and therefore not significantly affected by overlap competition), a correlation should be seen between the amount of specialization of individuals and the amount of morphological variation of individuals.

This theory can be applied to the group of species which are members of an ecological community with Black-capped Chickadees. The object would be to determine what kind of resource base the community is feeding on by testing for a correlation between the amount

of pursuit of food and morphological variation. This would indicate whether or not ecotypic selection is present and whether or not the resources are continuous. We would then have an idea as to the importance of overlap competition in chickadee population regulation. With this information, more effective management programs to regulate or increase chickadee numbers could be suggested.

Before this theory can be applied, however, a method must be found for measuring the amount of pursuing done by a species. Fretwell (ms.) provided a basis for use of measurements of the length of the catching apparatus as a measure of the amount of pursuing done by a species. The catching apparatus is that part of a predator's anatomy that first grabs and holds the prey before the predator actually puts the prey in its mouth. Some examples are beaks, talons, tongues, fingers, and any other structure used to grab prey.

Fretwell predicted that the catching apparatus of a searching species would be shorter than that of a pursuing species, if all other factors affecting catching apparatus size are constant or corrected for. This prediction is based on the different strategies of prey, and the strategies required of predators feeding on this prey. The relation between the variables of prey strategy, predator strategy, catching apparatus and ecotypic variation is summarized in Figure 1.

Prey can have the strategy of being hard to find, in which case it is relatively easy to catch. This is because the ways of becoming hard to find, like freezing, or wedging into a deep hole, require that the prey stay put and let the predator come right up. If the

predator does detect the prey, then he can usually catch the prey also. This type of prey is usually hunted by searching, generalist individuals, since a search is required to catch them.

Prey can also have the strategy of being hard to catch, but since this strategy requires that they move to avoid the predator well in advance of his approach and thereby make their whereabouts known, they are not hard to find. Prey with this strategy will evolve to become more and more hard to catch. Since this type of prey must be chased to be caught, they are usually hunted by pursuing, specialist individuals.

Since the prey of a searcher is easy to catch, he does not need a long structure to help him catch it. And in the case of avian predators, the consideration of weight will probably mean that he will not have it.

The prey of a pursuer, on the other hand, is usually fast and agile. As the predator is closing in, a slightly longer catching apparatus might make the difference between catching and missing, so a pursuer will tend to evolve a longer catching apparatus.

Another factor that needs to be taken into consideration is the relationship between average prey size and the size of the predator's body and catching apparatus. Predator body size correlates with average prey size in insect-eating birds (Hespenhiede, 1971a), and body size of the predator also correlates with length of the catching apparatus (Fretwell, pers. comm.). Therefore, a predator that takes large prey would have a large catching apparatus due in part to these relationships and not entirely because of a relationship

between the length of the catching apparatus and amount of pursuing done. The way to correct for the effect of body size (and the indirect effect of prey size) on the length of the catching apparatus is to divide the length of the catching apparatus by some measure of body size of the predator, thereby getting a relative measure of catching apparatus length. This corrected length would be predicted to be constant in species which all do the same amount of pursuing.

Fretwell tested the prediction of relative length of the catching apparatus correlating with the amount of pursuing in three groups of insect-eating birds: flycatchers, a group of pursuing species; swifts, a group of searching species; and swallows, a group of intermediate species. The prediction was confirmed between groups, with flycatchers having longer bills, relative to their body size, than swallows, and swallows, longer than swifts.

Preliminary Test of Theory: the Case for Hawks and Falcons

For my study, I wished to reconfirm this relationship in another group of ecologically related species whose feeding strategies have been verified by field work. The Accipiter, Buteo, and perhaps Falco predatory birds fit this requirement, so they were used for a test of the use of the relative size of the catching apparatus as a measure of the amount of pursuing done by members of a species or a group of species.

It is obvious that accipiters should be considered pursuers, and buteos, generalists, but the strategy of the falcons was less clear. However, the percentage of birds in their diets is intermediate between that of accipiters and buteos, so I decided to consider them intermediate pursuers. According to the predictions made above, accipiters should have the longest catching apparatus, falcons next, and buteos last.

Detailed information about the feeding habits of three accipiters, A. gentilis, A. cooperii, and A. striatus, allowed predictions about the size of the catching apparatus of species within this group. A. gentilis should have the smallest catching apparatus, since members of this species take more mammals, which are easy to catch but hard to find compared to birds. A. cooperii takes an intermediate proportion of mammals, and so should have the intermediate sized catching apparatus, and A. striatus, who feeds almost entirely on birds, should have the largest catching apparatus. All predictions

concern size of the catching apparatus relative to body size and assume a constant prey size to predator size ratio.

If measurements of the size of the catching apparatus do prove to reliably reflect the amount of pursuing done by a species, then a test of the prediction of the theory of ecotypic selection that pursuers will be more variable than generalists can easily be made. All that is necessary is a measure of morphological variation. The specific predictions to be tested were that accipiters would be most variable, falcons next, and buteos last.

Materials and Methods. Since hawks catch their prey with their feet, some measure of foot size seemed suitable. Hind talon length, divided by bill length (a suitable measure of body size for hawks) to make the measure a relative one, was used.

I measured talon length along the outside of the talon from the tip to the edge of the skin with vernier calipers. Bill length was measured from the tip to the proximal edge of the nostril. Wing length was used in estimates of coefficient of variation because (1) wing length reflects body size, which is correlated with prey size and, (2) wing length, being a bigger morphological entity, has relatively less measurement error than talon or bill. This reduces the measurement component of variability to a minimum. It was measured as the distance from the top of the wrist to the end of the longest unflattened primary. The specimens were from the University of Kansas Natural History Museum. The species measured were: Accipiter striatus, A. cooperii, A. gentilis, Buteo platypterus, B. jamaicensis, B. lagopus, Falco sparverius, F. columbaris,

F. mexicanus, and F. rusticolus. Number of specimens of each species varied and depended on the number available (see Table 1). Damaged, worn, and very young birds were avoided, but birds from all over the United States were used.

One of the assumptions required for the use of relative length of the catching apparatus as a measure of amount of pursuit is that the relation of prey size to predator body size is constant between species in a group, so that when the length of the catching apparatus is divided by a measure of body size, which reflects prey size, all effects of prey size on catching apparatus size will be corrected for and the only variable affecting catching apparatus size is the amount of pursuing done by a species. However, in the accipiters, the relationship between prey size and predator body size is not constant, but increases with predator body size (Storer, 1966). In other words, A. gentilis take larger average prey for their body size than do A. cooperii, a smaller hawk, and A. cooperii take larger prey for their body size than do A. striatus, an even smaller hawk. Therefore, dividing catching apparatus size (talon length) by a measure of body size (bill length) would not correct completely for the effect of prey size on talon length in these hawks, and amount of pursuit would not be the only variable affecting catching apparatus size.

A graph of the talon length divided by the bill length of the above hawks against an independent measure of body size, wing length (Figure 2), shows that, even after talon length is corrected for body size, talon length still increases with body size as measured

by wing length. To deal with this effect, I took a regression of body size for accipiter individuals against relative talon length. This line describes the expected value that relative talon length would take at any wing length is body size, as measured by wing length, alone is the determinant of relative talon length.

The amount of pursuing done by a species involved will cause deviations of each species' mean values from the regression line. I added these deviations to the mean talon length for all accipiters to make them comparable to other hawk groups. This provided a corrected value for relative talon length of each species. This corrected value would be treated just like any other relative talon value, and could be expected to correlate with the amount of morphological variation as measured by coefficient of variation of wing length in an ecotypically selected species.

A. cooperii individuals were selected as the group of accipiter individuals that would prescribe the regression line to be used as the expected value of relative talon length at a given body size (see Figure 2). The reason for this is that the regression of relative talon length against body size in A. cooperii had a slope higher than that seen in either of the other two species and in an average for all three species. This analysis involves rather narrow ranges of data, and a truncation bias can seriously affect the results. In the Cooper's Hawk data, the range of abscissa values is largest, relative to the range of ordinant values, minimizing this truncation effect. This regression line was plotted through a point determined by the average talon to bill ratio and the average wing

length for the accipiters. The deviation of the real average talon-to-bill ratio from the expected value of the talon-to-bill ratio at the average wing length were taken for each species, and this deviation, complete with sign, was added to the average talon-to-bill ratio for all accipiters.

Talon-to-bill ratio, corrected for the accipiters, was plotted against coefficient of variation for wing length for all species, as a test of the prediction of the theory of ecotypic selection that pursuing species will show greater variability in body size.

Results and Discussion of Hawk Investigation

The predictions about relative talon length were partially confirmed between groups and completely confirmed within groups. Accipiters had the longest talons, and buteos had talons smaller than accipiters, as predicted (see Figure 3). However, the falcons had talons even shorter than the buteos, which was not predicted. Further reading convinced me that the falcon method of catching prey would make talon length comparisons difficult between falcons and the other groups. Falcons often dive on preselected prey and stun the prey with a blow (Brown and Amadon, 1967). This dive is often at very high speed, and is different from the way accipiters and buteos grab their prey.

Within the accipiter group, the predictions were confirmed. A. striatus had the longest talons, A. cooperii next, and A. gentilis last. Within the falcon group, a prediction of smaller talons for more generalist species seemed to be confirmed, also. F. sparverius takes a wider variety of prey items than any of the other falcons and had the shortest talons. F. columbaris takes the next widest variety of prey items and had the next shortest talons.

A plot of coefficient of variation of wing length against talon-to-bill ratio showed a positive overall trend between groups and stronger trends within groups. The between-group trend, when only accipiters and buteos were considered, was strong and verified the prediction that there is a correlation between amount of pursuing

done by a species and the variation of body size. However, the short talons of the falcons made the fit less precise.

My conclusion, then, from this exercise with the hawks, is that the feeding apparatus can be used as a measure of the pursuing done by a species, and that the amount of pursuit done by members of a species, as reflected by the size of the feeding apparatus, correlates with variation in ecotypically selected populations. However, since differences in hunting methods between groups can cause variations in the length of the catching apparatus not entirely related to amount of pursuing done by a species, within group correlations may be the most precise.

Because the use of morphology as a measure of pursuit done by a species has now been confirmed, I should be able to apply this technique to the winter woodland insect-eating community I am interested in and use the size of the feeding apparatus as a measure of pursuing here also. If the species in this community are ecotypically selected, then the size of the feeding apparatus should correlate with variation in body size.

The Woodland Community

The amount of overlap competition constraining chickadee populations can be measured indirectly by applying the theory of ecotypic selection to the winter woodland community of which the chickadee is a member. If the predictions of the theory of ecotypic selection are true for the species of this community, then the resource base would be a discrete one and overlap competition would not be a factor in chickadee population regulation. If, however, the predictions are not verified for some or all species of the community, then at least some of the species are simultaneously utilizing a continuous resource base, and so would constrain each other by overlap competition. If the chickadee were one of these species for which the predictions were not verified, then overlap competition would be considered to be a factor in chickadee population regulation.

If this community is ecotypically selected, then the pursuing species with specialist individuals will be more variable than searching species with generalist individuals. Since the catching apparatus of an insect-eating bird is the bill, relative bill size should index the amount of pursuing done by a species, as relative talon length was with the hawks and relative bill length was for the Flycatchers, Swallows, and Swifts. Therefore, I would try to find a correlation between bill length and morphological variation (again measured by coefficient of variation of wing length).

In addition, if this community is ecotypically selected, then

consumers of dense resources, themselves dense if they are not predator limited, should be pursuer-specialists. Therefore, I would expect to find a correlation between density of the predator and morphological variation as Rothstein (1973) and Fretwell (1972) have done.

Materials and Methods. Bill length from the tip to the distal edge of the nostril and wing length from the top of the wrist to the tip of the longest unflattened primary were measured on University of Kansas Natural History Museum specimens of Golden-crowned Kinglets, Yellow-rumped Warblers (Dendroica coronata), Black-capped Chickadees, Tufted Titmice (Parus bicolor), Blue Jays (Cyanocitta cristata), Red-breasted Nuthatches, White-breasted Nuthatches, Brown Creepers, Carolina and Winter Wrens (Troglodytes troglodytes and Thyrothorus ludovicianus), and Downy, Hairy, and Red-bellied Woodpeckers (Dendrocopus pubescens, D. villosus, and Centurus carolinus). All specimens were taken in the months of March through December, and, except the Yellow-rumped Warblers which were taken near Van Buren, Arkansas, all were taken in Douglas, Johnson, or Jefferson counties of Kansas, with the great majority taken in Douglas County. Yellow-rumped Warblers were taken in Crawford County, Arkansas. A rough estimate of density was made with the use of Kansas Ornithological Society Mid-winter Bird count data for Douglas County (1954-1960, 1968-1972), and Audubon Society Christmas Count data for Crawford County, Arkansas (1960-1970).

Data Analysis and Results. For my first analysis of the data I used the average coefficient of variation of wing length for each

species as a measure of variation. A plot of this against density and against bill length corrected for body size showed no discernable trend. However, the density axis was severely truncated as compared to the one in a graph for sparrows by Fretwell (ms.), where a correlation was seen. If his graph were truncated similarly, it would not be significantly different from mine.

My next graph, a plot of coefficient of variation of bill length against density (Figure 4) did not show a positive slope when all species were considered together, but positive slopes were seen within groups of gleaners, wood creepers (creepers and nuthatches together), Wrens, and Woodpeckers. The lack of an overall positive correlation on this graph may also be explained by the severe truncation of the density axis.

A graph of coefficient of variation of bill length against relative bill length (bill length cubed over average body weight) showed a positive trend, implying that species did become more variable with higher pursuit ratios, and that ecotypic selection was a force in the community (Figure 5). However scatter was wide, and the positive trends were stronger within groups than in all species considered together. This indicated that membership of a species in groups was, for unknown reasons, having an effect on both density and bill length independent of a relationship with variation.

The original coefficient of variation of bill length against density graph showed many species at the far left of the graph, and the within-group slopes tended to be steeper in this region, overall. For these reasons I converted to a natural logarithmic scale

for density (Figure 6). I then took an average of all the within group slopes on this graph, and corrected for the overall density effect by taking the deviations of each species from a line of average slope, plotted through an average point for each group. These deviations reflect whether or not a species is more or less variable than it should be according to its density, and, in an ecotypic community, should correlate with the amount of pursuing done by a species. To test this, I plotted these deviations against the natural logarithm of relative bill length for each species (Figure 7).

I analyzed this final graph by finding an average slope for the groups, and noting the deviations of each species from its group line, plotted through an average point for each group. Wrens had to be dropped from the analysis at this point, since I was unable to find an average weight for Winter Wrens in the literature. This graph showed that approximately seventy per cent of the scatter of coefficient of variation of bill length was from the effect of density, plus the effect of pursuing (specializing) plus the effect of falling into feeding type groups.

A multiple regression was performed with four independent variables. These were natural logarithm of density, natural logarithm of bill length cubed over average body weight, the quality of being a gleaner and the quality of being a Wood Creeper. The dependent variable was coefficient of variation of bill length. I found a statistically significant partial regression of coefficient of variation of bill length against relative bill length, confirming the prediction that variation will increase with increased degree of

pursuit of prey, and indicating that this community is at least partially under ecotypic selection. The amount of scatter of the coefficient of variation of bill length that this regression explained was 68 per cent.

DISCUSSION

Throughout this analysis, the species I am interested in, the Black-capped Chickadee, showed consistently lower variation than could be explained by search-pursuit ratios, density, or membership in the gleaner group. This suggests that the gleaner group is at least partly dependent on a continuous resource base, and therefore not all its members are ecotypically selected. However, some members of the community (Blue Jays, for example) are apparently ecotypically selected and dependent on a discrete resource base.

MacArthur and Levins (1967) developed a model showing that in a species-rich community, jacks-of-all-trades (intermediate-sized species) would be present, along with larger and smaller sized species. In a species-poor community, on the other hand, only extremes would be present, if the species were on continuous resources. Another model, developed by MacArthur and Levins in 1964, showed that for species on discrete resources exactly the opposite is true. That is, in a species-poor community, extremes are lost and only intermediate sizes are left, and species-rich communities have many extremes and few intermediates. Applying these models to the gleaner group indicates such species may usually be on discrete resources. In species-rich communities (Great Britain and Europe) there are many species of titmice of an intermediate size, Black-capped Chickadee size or slightly larger but smaller than the Tufted Titmouse. In a species-poor community (North America) there are

essentially only the two extremes. Also, in the Northern part of the United States, the Tufted Titmouse is lost, apparently squeezed out by overlap competition with jays and chickadees which have more northern ranges.

The implications of this for chickadee management is that factors causing an increase in titmouse numbers should cause a decrease in chickadee numbers. If some factor tends to cause an increase in both chickadee and titmouse numbers, like a winter feeder, however, then the increase of both populations will be slowed. Support of this idea is that winter feeders do cause only a slow increase in chickadee numbers (Hammerstrom, 1941).

Fretwell (1972) developed a model for Fringillid body size in which body size increases with seed size because of the difficulty a small bird has in utilizing a large seed. When I tried to analyze this insect-eating community using coefficient of variation of wing length, however, my results were inconclusive. A possible explanation for this is that the energy required to utilize insect matter may not vary as strongly with resource size as it does for seeds, so that consumer body size as reflected by wing length may not vary as significantly with insect-eaters as it does in seed-eaters.

Hespenheide (1971a), however, found stronger correlation of food size with wing length than with bill size in the Tyrannidae. My results are inconclusive on this point which should be investigated further.

CONCLUSION

There is a rich literature on the natural history of the Black-capped Chickadee, since it is a popular and easy bird to study. I attempted to fill some gaps in the knowledge of the population regulation of the chickadee by applying the theory of ecotypic selection to the winter woodland insect-eating community in Kansas, of which the chickadee is a part.

I determined, with the use of groups of hawks, that size of the catching apparatus gives an index to amount of pursuing of prey done by members of a species and that this index will correlate with variation of body size in an ecotypically selected community. I applied this knowledge to the woodland community and found indications that this community is at least partially ecotypically selected, and so some species are feeding on discrete resources. However, the chickadee seems to depend to some extent on continuous resources, which it shares in overlap competition with the Golden-crowned Kinglet and the Tufted Titmouse. If this is the case, then the chickadee would be affected by competitive constraint from these and other ecologically related species. Also, factors causing an increase in populations of these species could cause a decrease in chickadee numbers.

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Figure 1. The relationship between the variables of prey strategy, predator strategy, catching apparatus size and ecotypic variation.

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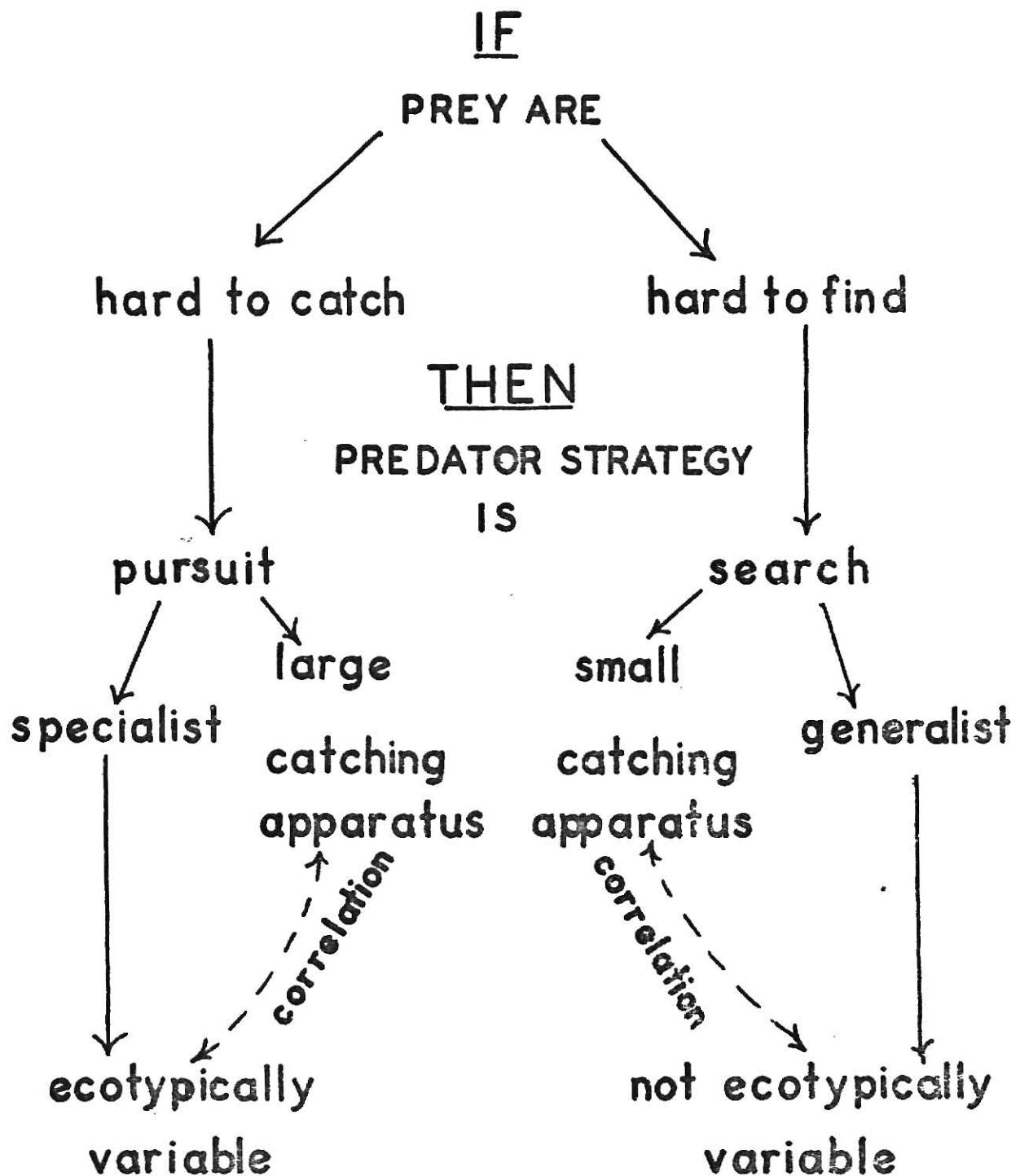


Figure 2. Relative talon length plotted against wing length for individual Accipiterine hawks.

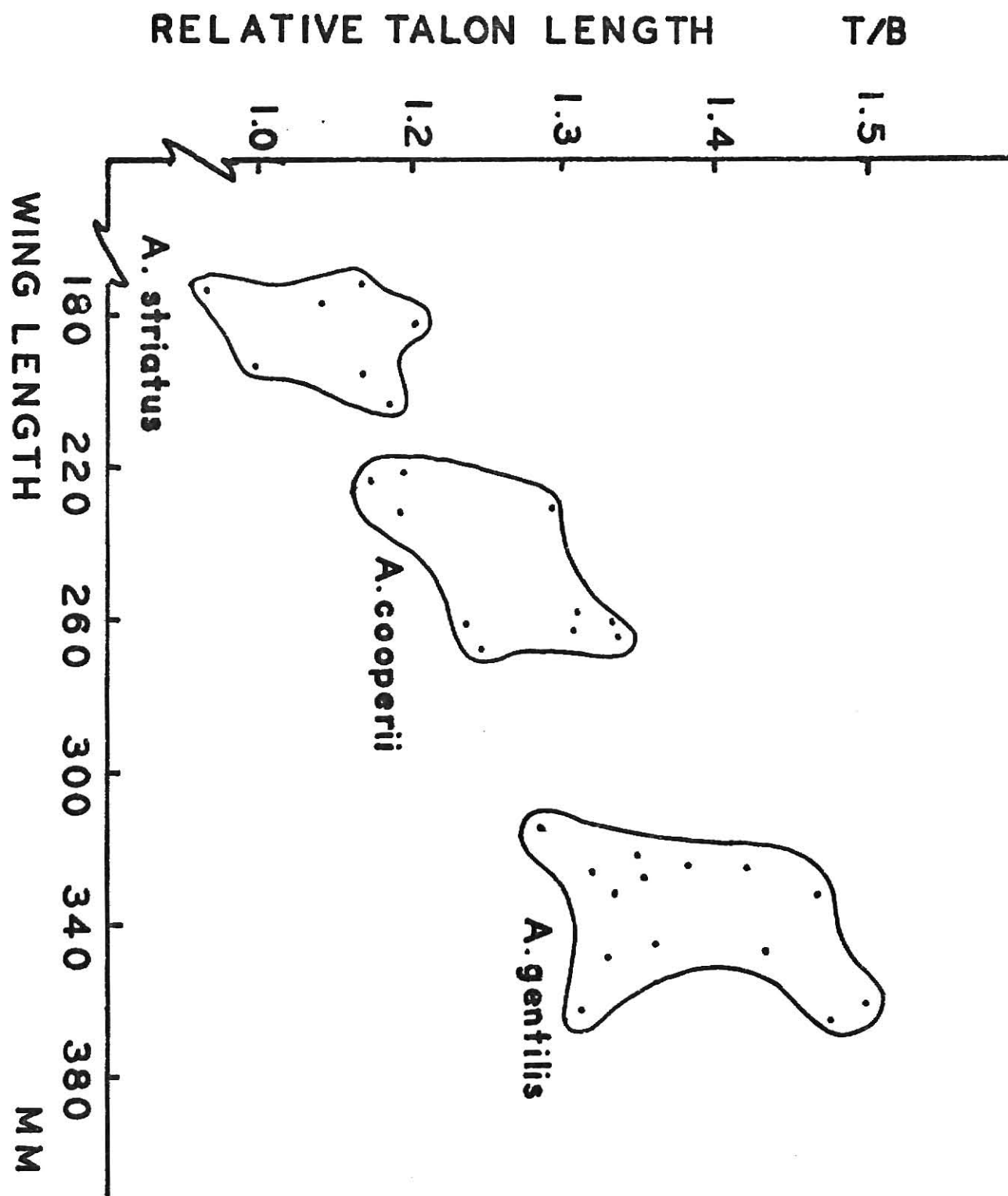


Figure 3. Coefficient of variation plotted against relative talon length for all hawk species measured.

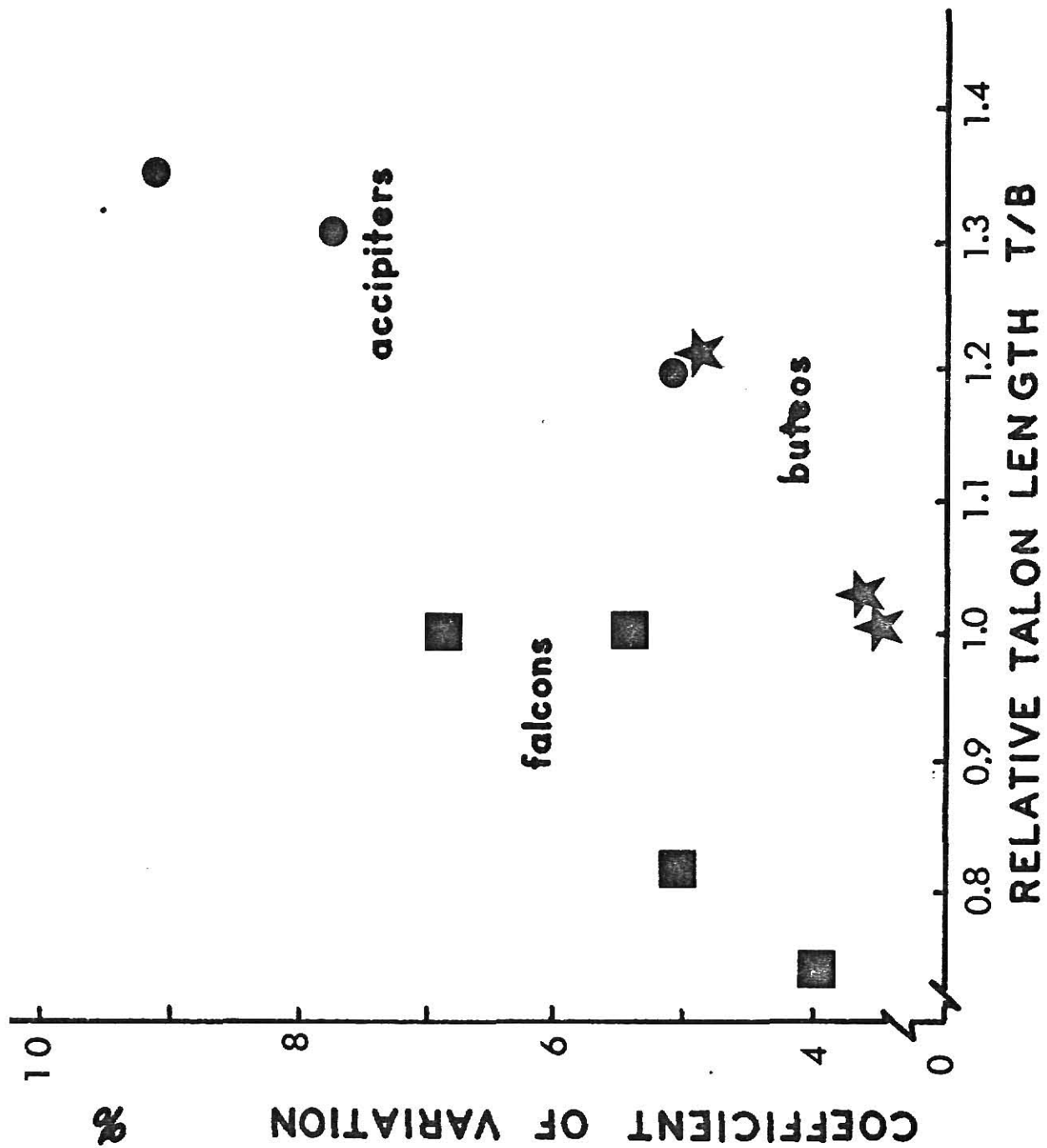


Figure 4. Coefficient of variation of bill length plotted against density for woodland species.

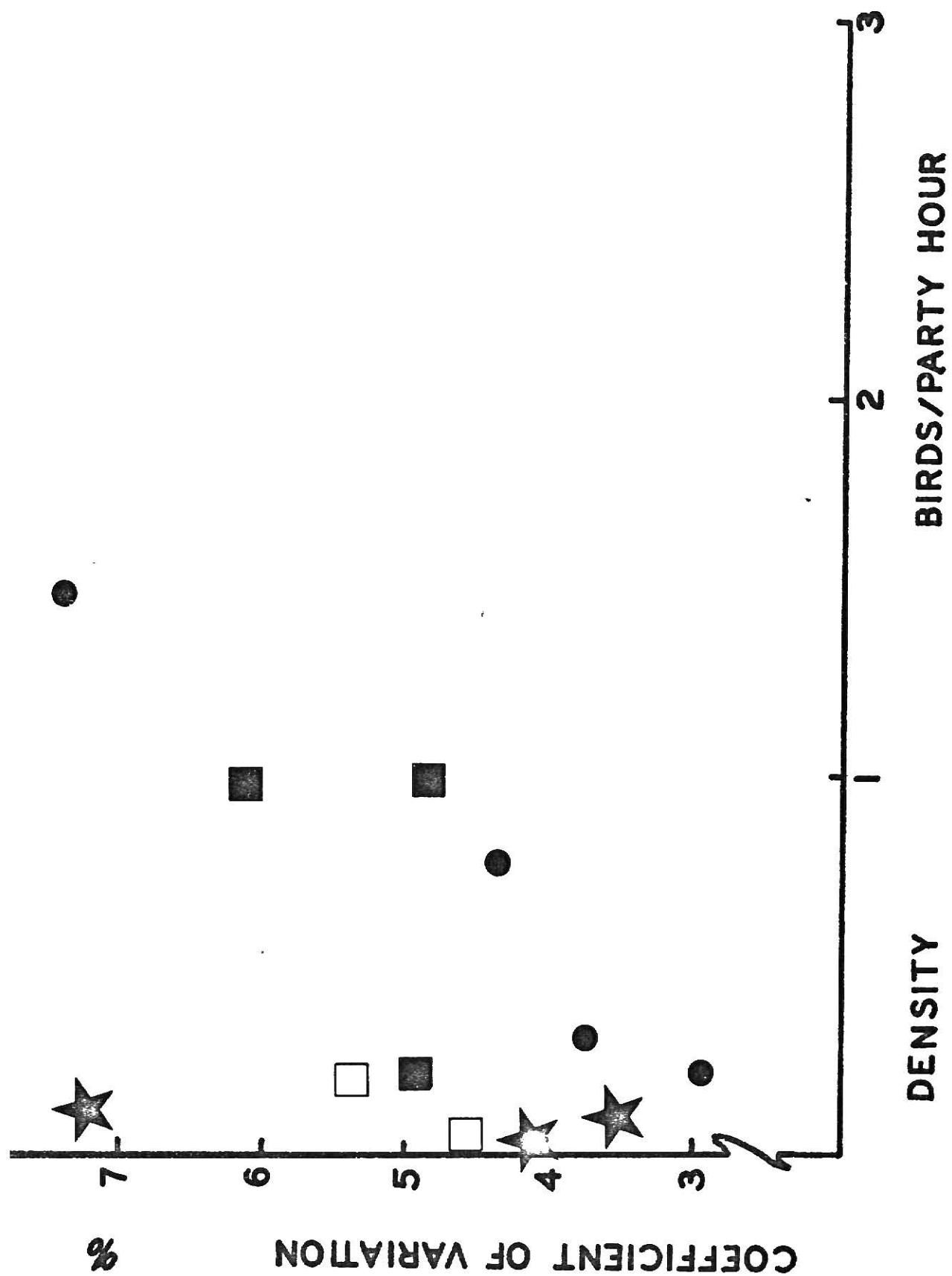


Figure 5. Coefficient of variation of bill length plotted against relative bill length for woodland species.

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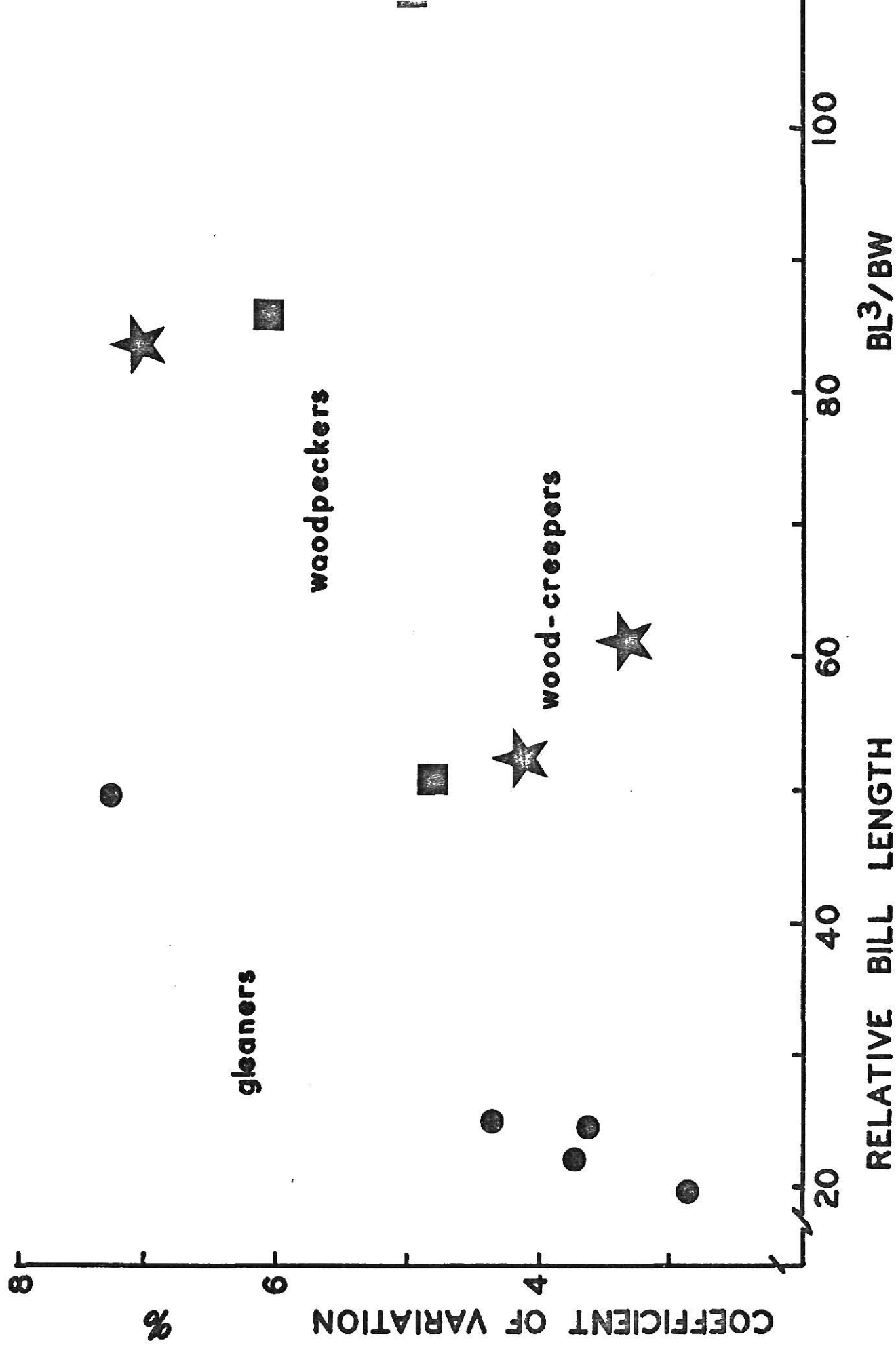


Figure 6. Coefficient of variation of bill length plotted against the natural logarithm of density for woodland species.

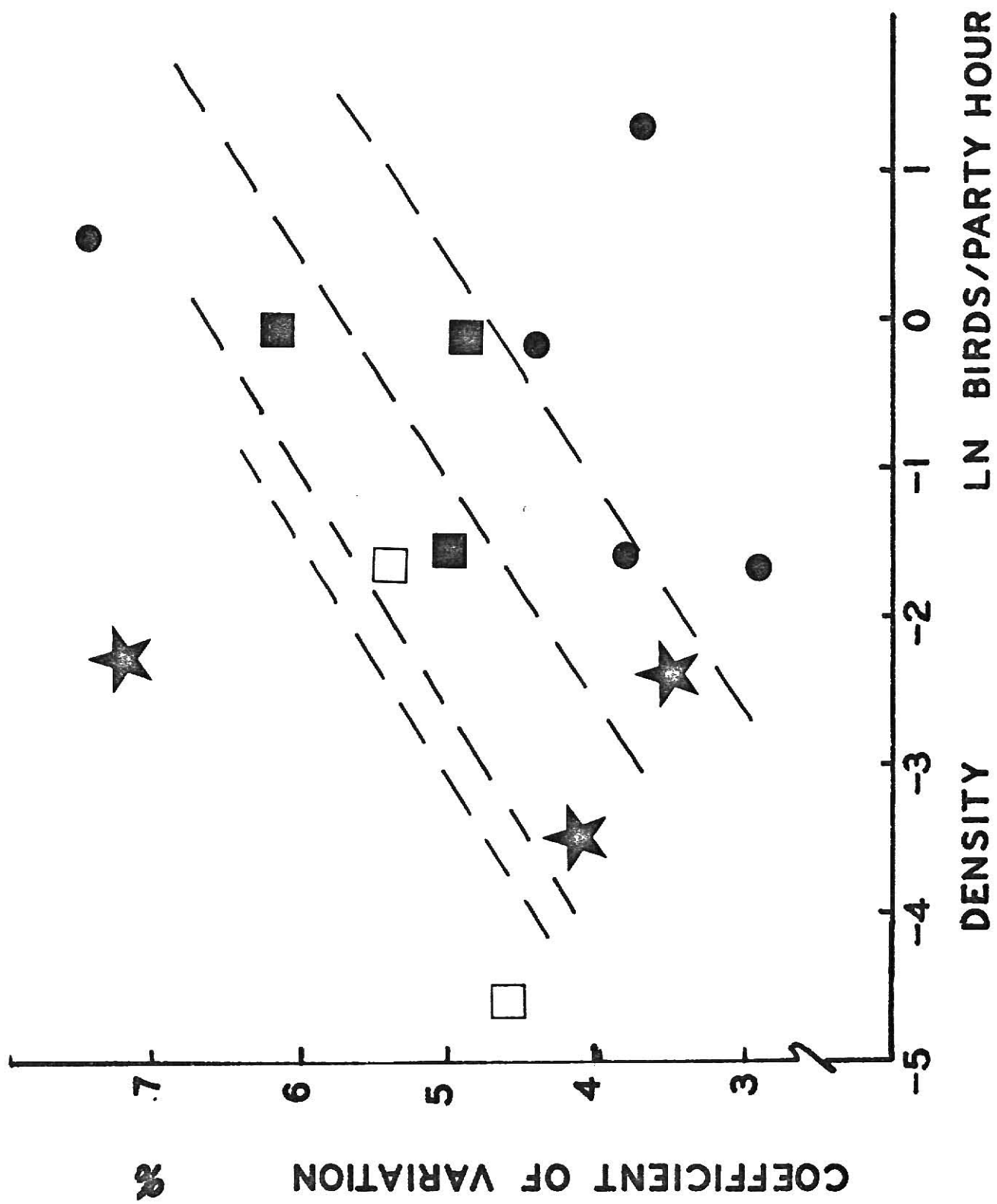


Figure 7. Coefficient of variation of bill length corrected for the effect of density and plotted against the natural logarithm of relative bill length.

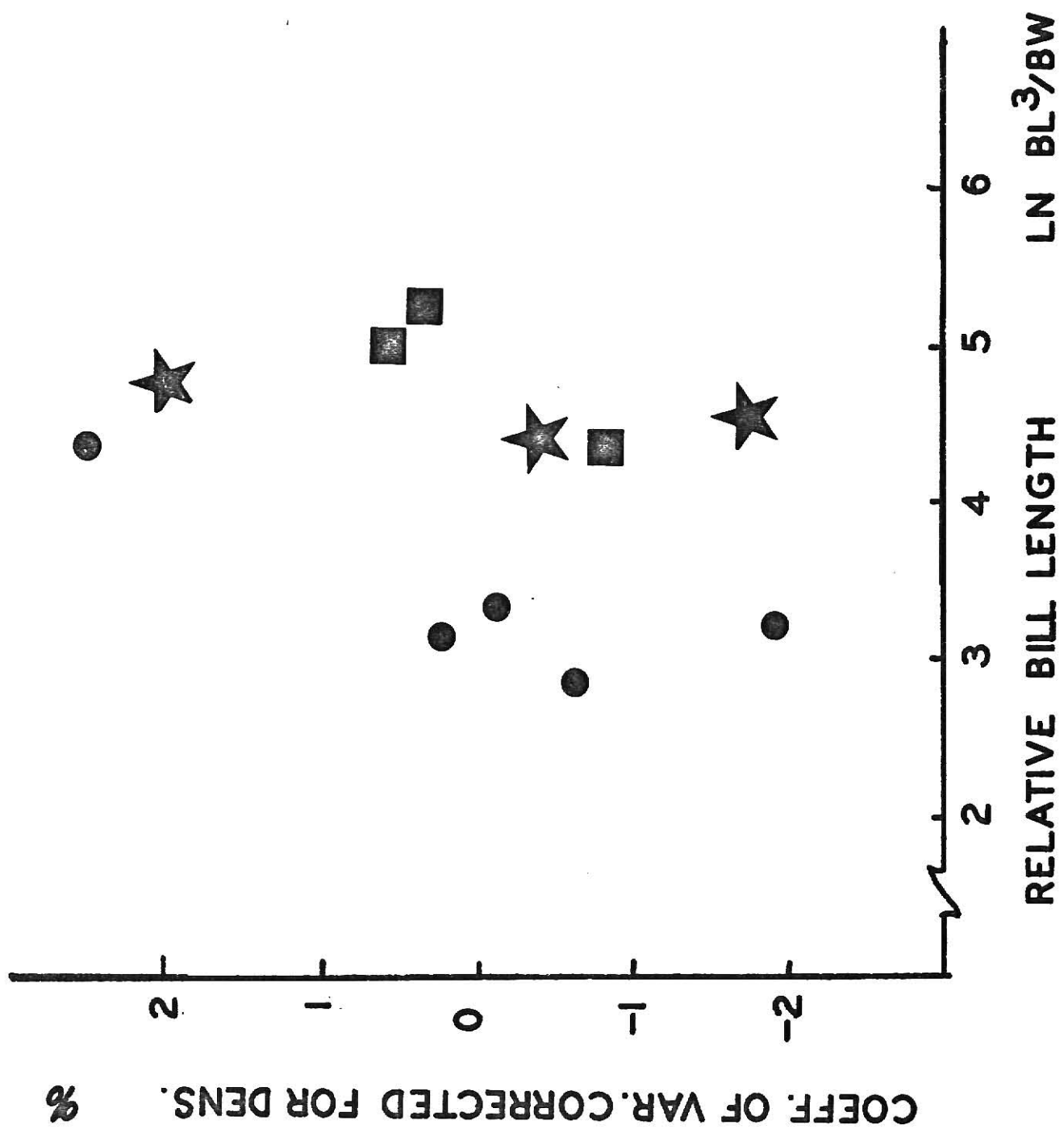


Table 1

Hawks

Woodland Birds

Species	No. ♂	No. ♀	C.V. winglength	Talon/Bill ratio	Species	No.	No.	C.F. winglength	Bill ³ /wt.
Accipiter striatus	17	31	0.0883	1.34	Black-capped chickadee	15	15	0.0361	28.2
A. gentilis	5	8	0.0500	1.18	Tufted titmouse	11	9	0.0436	29.9
A. cooperii	16	18	0.0788	1.31	White-breasted nuthatch	8	11	0.0347	102.5
Buteo lagopus	13	10	0.0366	1.10	Hairy woodpecker	5	7	0.0495	200.5
B. jamaicensis	11	19	0.0464	1.21	Downy woodpecker	10	10	0.0481	79.9
B. platypterus	4	11	0.0363	1.01	Blue jay	7	14	0.074	79.2
Falco mexicanus	5	9	0.0683	0.99	Red-bellied woodpecker	9	10	0.0609	152.0
F. sparverius	15	15	0.0398	0.73	Yellow-rumped warbler	5	1	0.0291	19.2
F. columbaris	7	9	0.0502	0.83	Red-breasted nuthatch	3	2	0.0409	85.1
F. rusticolus	5	5	0.0524	1.01	Golden-crowned kinglet	9	0	0.0376	23.8
					Brown creeper	12	10	0.0729	147.9

POPULATION REGULATION AND THE BLACK-CAPPED CHICKADEE
(PARUS ATRICAPPILLUS): A THEORETICAL DISCUSSION
AND AN APPLICATION OF THE THEORY OF ECOTYPIC SELECTION

by

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A review of the literature on the natural history of the Black-capped Chickadee (Parus atricapillus) is presented as an annual cycle. Throughout the annual cycle, certain theories of population regulation, including theories of range, behavioral population regulation, clutch size, density-dependent seasonal regulation, and ecotypic selection, are discussed as they apply to the annual cycle.

The theory of ecotypic selection and the validity of the method of using catching apparatus length as a measure of specialization is tested with buteo and accipiter hawks and falcons. A correlation between length of catching apparatus and morphological variation is predicted, and the prediction is confirmed within groups and partially between groups.

The confirmed theory and method is then applied to the community of winter woodland insect eaters, of which the Black-capped Chickadee is a part. Species included in this test are: Golden-crowned Kinglet (Regulus satrapa), Yellow-rumped warbler (Dendroica coronata), Tufted Titmouse (Parus bicolor), Black-capped Chickadee (Parus atricapillus), Blue Jay (Cyanacitta cristata), Brown Creeper (Certhia familiaris), Red-breasted Nuthatch (Sitta canadensis), White-breasted Nuthatch (Sitta carolinensis), Downy Woodpecker (Dendrocopos pubescens), Hairy Woodpecker (Dendrocopos villosus), and Red-bellied Woodpecker (Centurus carolinus). Results indicated that density and grouping of species into woodpeckers, gleaners, and barkcreepers was having an effect, so these factors were corrected in a partial multiple regression. The regression showed a significant correlation

between coefficient of variation of wing length and relative length of the catching apparatus after the effects of groups and density were corrected for.

The conclusion drawn is that members of this community are ecotypically selected, on the whole, but that certain species, especially those in the gleaner group, may not be entirely ecotypically selected. When this conclusion is related to the resource base of the community, it appears that Black-capped Chickadees may be in part dependent on continuous resources, and therefore vulnerable to overlap competition from other species in this group of gleaners. This has significance for management of this species, since factors affecting the growth of other gleaner species could bring about a change in the numbers of Black-capped Chickadees.