THE OVERLAP OF MOLTING AND BREEDING IN SOME TROPICAL BIRDS

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Studies of temperate and tropical land birds reveal that the resource-demanding activities of the life cycle generally are mutually exclusive in an individual (Miller 1963, Farner 1964, Fogden 1972). Presumably food (calories, specific organic or inorganic nutrients, or the time to gather them) is limiting, and temporal spacing has evolved in response to the high requirements of each event. Thus an activity is timed to occur when environmental conditions are favorable and when interference from other activities is minimal.

Molt and reproduction are two of these resource-demanding events. Thus, I was surprised to find that a significant number of birds which I collected during several months of field work in Costa Rica were both breeding and molting. A review of the literature reveals that among tropical birds at least, molt-breeding overlap is more common than is generally supposed.

In this paper I will present new data on instances of overlap in breeding and molting in several neotropical species and list other tropical forms also reported to show overlap. Sources of energy and nutrients necessary for molt during breeding and advantages of overlap will be considered briefly.

METHODS AND MATERIALS

During 1967, 1969, 1971, and 1972, I spent a total of 16 months doing field work in Costa Rica. Incidental to this, I collected 780 specimens of 217 species of birds from various parts of the country, though most are from one locality (Finca Jiménez). Data from an additional 154 specimens (including 12 species I did not sample) collected by Carolyn Cavalier Boyd at various localities in Costa Rica during 1967 also were reviewed. Robert E. Ricklefs provided data for 26 specimens he collected in Costa Rica between 7 and 13 May 1971. Included were four species I had not collected. Representatives of all species or families present in the areas where I worked were not collected, nor were particular species collected regularly through the entire period.

Localities in Costa Rica from which specimens are reported and the life-zone in which they are situated (Tosi 1969) are: (I) Estación Experimental Enrique Jiménez Nuñez (Finca Jiménez), at Hacienda Taboga, Guanacaste Province (also 0.8 km and 1.6 km SE and 1.6 km E), in Tropical Dry Forest. (II) Estación Experimental Los Diamantes, approximately 1.6

km E Guápiles, Limón Province, in Tropical Wet Forest. (III) Finca Helechales, 12.5 km NE Potrero Grande, Puntarenas Province, in Premontane Wet Forest. (IV) Tropical Science Center Field Station, 4 km W Rincón de Osa, Puntarenas Province, in relatively undisturbed Tropical Wet Forest. (V) Finca El Silencio, Guanacaste Province, Premontane Wet Forest. (VI) Methodist Mission, Tesalia, 4.7 km NE Ciudad Quesada, Alajuela Province, in Tropical Wet Forest, Premontane Belt Transition. (VII) Road to Colonia La Virgen, 2.4 km to 4.0 km SE Cariblanco, Heredia Province, Premontane Rain Forest. (VIII) Río Toro Amarillo, approximately 6.4 km W Guápiles, Limón Province, in Tropical Wet Forest. Roman numerals may be used to denote localities in species accounts.

Only the presence of sheathed feathers, which were assumed to be growing, was used as an indication of molt. Replacement of remiges and/or rectrices was noted for each specimen; degree of body molt was determined subjectively according to the number of feathers and feather tracts involved. In birds with light body molt, less than 20% of the body feathers were at least partially ensheathed. In those with moderate molt, approximately 20–40% of the feathers among several tracts were growing; in those with heavy molt, more than 40% of the feathers were being replaced. Only birds exhibiting approximately symmetrical replacement of feathers were included. Birds replacing no flight feathers and so few body feathers that loss could have been accidental were excluded. In specimens which I collected, the length and width (or length only) of the left testis or the diameter of the largest ovarian follicle was measured in millimeters. All birds were examined for the presence of a brood patch and females for oviduct enlargement. Testes from many males collected in 1971 and 1972, representing nine of the species reported here, were preserved, sectioned at 7 μ, stained with hematoxylin and eosin, and examined microscopically. These were staged according to the scheme presented by Payne (1969a). Data for specimens I did not collect were supplied by the collector. Nomenclature follows Eisenmann (1955) and Meyer de Schauensee (1966).

Specimens are deposited in the Museum of Vertebrate Zoology (MVZ), University of California, Berkeley, and in the skeletal collection of the Department of Biology, University of South Florida, Tampa.

The Chi-square method of ratio testing was used for comparisons.

CRITERIA FOR BREEDING

Females were considered to be breeding if they had enlarged or enlarging ova, an enlarged oviduct, or an active brood patch. Males were considered to be breeding if the testes showed sperm in the Sertoli cells and free in the lumina (Stage 7 of Payne 1969a). Associated observations of behavior, body size, intraspecies comparison of specimens, and data from the

literature were used in selecting the testis size indicative of breeding in males whose testes were not sectioned.

Several authors (Moreau 1936, Miller 1962, Snow and Snow 1964) have noted that males of tropical species often maintain enlarged testes for relatively long periods even though the actual breeding period is sharply delimited by the reproductive state of the female. Consequently, many authors use only the presence of eggs or nestlings as a true indication of breeding. This is probably a valid limitation for the determination of the true breeding period of a population or a species. With regard to resource expenditure for reproduction, however, more latitude may be permitted, particularly with reference to males. For example, males of the Rufous-collared Sparrow (*Zonotrichia capensis*) sing, court, and maintain their testes at breeding level for long periods during which their female partners do not nest (Miller 1962). Thus, even if males are not actually breeding (and this is difficult to determine for some species, for example, those with no persistent pair bonds), energy expended on testes maintenance, sperm production, and especially on singing, displays, territorial defense, and other activities usually stimulated by sex hormones (Kendeigh 1941, Miller 1958, King 1972a) may be important.

Related to this is the phenomenon of incomplete gonad regression, which apparently is common among tropical forms. Among females of many species, inactive ovaries of extremely small size are found only in immature individuals; ovaries of adult females contain enlarged follicles (1.0–1.5 mm diameter) at all times (Bates 1908, Miller 1962, Foster, in press). A similar phenomenon is found in males of many tropical species in which the annual range of testis size is smaller than in temperate forms, presumably because of a higher minimum rather than a lower maximum size (Moreau et al., 1947, Maclean 1973). Payne (1969b) also suggested that a smaller amplitude of seasonal change in gonad size occurs in several African birds that appear to exhibit relatively incomplete regression in the nonbreeding season. I found this for several neotropical species, too. Thus, it is often impossible to predict the internal condition of the testis on the basis of whole-organ measurements except for extremely small testes that are dormant. Spermatogenesis commonly is evident in testes well below maximum size. The significance of such incomplete regression is not clear. Also typical of many tropical forms is the unusually long period of male reproductive activity. When these phenomena are considered together, it is evident that for the major part of the year, males are appproaching or are in reproductive condition.

As females of many species are reproductively active for only a short period each year, the significance of the extended reproductive period of males may be related to some other activity. Perhaps the absence of long-distance migration makes tremendous decrease of gonad size as an adaptation for weight reduction unnecessary for most tropical forms. Alternatively, the conservation of energy or specific nutrients required for gonadal recrudescence may be important. However, incomplete regression probably has a more positive function. Many tropical species are quite sedentary. Thus, it may be important for them to maintain territories or positions in a dominance hierarchy throughout the year. Some tropical birds remain paired all year, occupying the nesting territory or at least maintaining contact with it

(Skutch 1949, Miller and Miller 1968). This might be particularly significant in those species in which some individuals are breeding at all times of the year. Thus, it is not unreasonable to assume that large testis size, though not necessarily indicative of actual breeding, may well be associated with activities of considerable energy expenditure.

In view of this, and because the presence of enlarged testes is usually the only available determinant for reproductive cycle stage of males at the time of collecting, I include in this paper all males with large testes, even those for which more definite breeding evidence was not available. As will be indicated in the analysis below, some of these were considered to be breeding, others merely to have incompletely regressed testes.

CRITERIA FOR MOLT-BREEDING OVERLAP

Although most birds undergo only one complete molt each year, many temperate species regularly replace all or a large portion of the body feathers more than once per annum (Dwight 1900, Foster 1967). This phenomenon has been noted less commonly in tropical species (e.g., Dickey and van Rossem 1938, Wolf 1969), but quite possibly this is only a reflection of our lack of knowledge. Thus, I do not consider valid the usual practice of most authors who have considered the question of molt-breeding overlap (e.g., Moreau 1936, Snow and Snow 1964, Payne 1969b) of disregarding such "incomplete" molts. Incomplete molts may be more difficult to distinguish from adventitious loss, but with some discrimination it is possible. Certainly, incomplete molts consume less energy than those which include flight feathers, at least in terms of replacement costs, but the amount is still substantial. Thus Newton (1966) found that in the Bullfinch (*Pyrrhula pyrrhula*), a temperate species, body feathers comprise 69.1% of the total feather weight, whereas remiges and rectrices and their associated coverts comprise only 22.4% and 8.5%, respectively. In addition, energy expenditures for thermoregulation may be similar for both molts.

SPECIES ACCOUNTS

Crypturellus cinnamomeus. Thicket Tinamou. A female, taken 18 May at Finca Jiménez, had a greatly enlarged oviduct and yolked ovarian follicles of 13, 6, and 4 mm. She was replacing scattered upper-wing coverts and low to moderate numbers of feathers in all body areas.

Jaçana spinosa. Wattled Jaçana. A female, taken on 4 June (I), was undergoing a moderate body molt dorsally and ventrally. Her largest ovarian follicle was 4 mm. For 30 min prior to collecting, I observed the female and two other individuals engaged in territorial and precopulatory displays (identified according to Jenni and Collier 1972). Two males, taken 12 August with testes of 14 × 7 and 19 × 10 mm, showed no sign of molt.

Columbina passerina. Common Ground-Dove. Five specimens were collected at Finca Jiménez between 11 and 18 August. Two females showed molt-breeding overlap. One had an 11-mm follicle and exhibited moderate to heavy replacement of body feathers; primaries 9 were completely ensheathed and 1-8 appeared new. Secondaries 1 and 2 were new, 3-3 and right 4-5 growing. The second female showed light body molt ventrally and held an oviducal egg with a fully formed shell. A third female was molting but not breeding. One male (testis 10 × 5) was not molt-

ing. A second (testis 8 × 4) showed moderate to heavy molt in all areas; primaries 1-8 appeared new and 9-9 were growing.

Columbina talpacoti. Ruddy Ground-Dove. A single male (testis 8 × 4) was taken at Los Diamantes on 26 July. It was replacing a moderate number of body feathers in all areas and several tertials on each wing. Snow and Snow (1964) studied this species in Trinidad where, in wetter areas, it bred all year. They found wing molt in nearly every month, but molt was arrested with the onset of breeding. They suggested that molt begins during periods unfavorable for breeding but is interrupted when local conditions again stimulate breeding.

Leptotila plumbeiceps. Gray-headed Dove. A male, taken 20 April at Finca Jiménez, had a testis 9 × 6 mm and was in heavy body molt dorsally and ventrally.

Crotophaga sulcirostris. Groove-billed Ani. Seven specimens were collected (I and II) between 20 July and 1 August. A female, taken 20 July, had an enlarged follicle of 3 mm. A male, taken 23 July, had a testis 10 × 6 mm. A male, taken 29 July, and two, taken 1 August, had medium-sized testes (6 × 4, 7 × 4, and 6 × 4 mm). Data on the labels indicate that the former two individuals, which were prepared as skeletons, were molting. Sandra Vehrencamp (pers. comm.), who is conducting an extended study of this species in Costa Rica, informs me that the anis molt slowly and fairly continuously over most of the year, even while breeding.

Morococcyx erythropygus. Lesser Ground-Cuckoo. Molt-breeding overlap seems to occur regularly in this species. Five specimens were taken at Finca Jiménez; only one (female, largest follicle 2.0 mm) was not molting. Two other females (19 July, 14 August) had ova of 3 and 4 mm (yellow-orange), respectively. Males taken on 14 and 18 August had testes of 6 × 4 and 5 × 3 mm. All four individuals were replacing one or more pairs of primaries, secondaries, and rectrices and many body feathers.

Three specimens (MVZ 153254–153256) from 4.0 km E Tehuantepec, Oaxaca, México, also exhibit overlap. Two males and a female, taken on 20 August, were in breeding condition (testis 6 × 4, brood patch stage 4; testis 5 × 3, ovarian follicle 9.5, ruptured follicle). One male was replacing only a single pair of rectrices; the other was in heavy body molt and replacing a pair of rectrices, a pair of secondaries, and three pairs of primaries. The female was growing one pair of rectrices and numerous body feathers.

Nyctidromus albicollis. Pauraque. Two males were collected at Los Diamantes on 25 and 27 July. Both were molting but not breeding. Four specimens were taken at Jiménez. Two females (15 July, 11 August) had inactive ovaries; the latter individual was molting. A male (14 August) with regressed testes (5 × 2) also was molting. A second male (9 June) with greatly enlarged testes (15 × 8) was replacing two pairs of rectrices, one pair of primaries, three pairs of secondaries, and numerous body feathers. Miller (1963) also found overlap in several Colombian Pauraques; a male, taken 13 April (testis 11 mm), showed some body molt. Another from 27 May (testis 9 mm) was in heavy molt including primaries.

Trogon massena. Slaty-tailed Trogon. A male, taken (I) 17 August with a testis of 7 × 3 mm, was just beginning to molt. Many new feathers were growing in the interscapular and interramal regions.

Trogon citreolus. Citreoline Trogon. A male (I), taken 25 April, was undergoing moderate replacement

over the entire body including the patagial and upper-tail coverts. His testis (6 × 3 mm), in stage 3, was only approaching breeding condition. Three males (7, 10, 19 July), with testes of 5, 6, and 7 × 5 mm, were undergoing light to moderate body molt; flight feathers were worn. A female collected on 18 July (largest follicle 2 mm) had ensheathed body feathers in all areas and rectrices 2, 3, and 4, primaries 5, and secondaries 1, 7, and 10 growing. Two males, taken 11 and 16 August, had testes of 10 × 7 and 7 × 5 mm. The former was molting lightly in all areas and rectrices 2 and 3 were growing. The latter exhibited moderate to heavy body molt, rectrices 1-3 were growing and 6 dropped, and secondaries 1, 8, and 10 were growing. Five females were taken on 1, 12, 14 and 17 (two) August. Their largest follicles measured 1.5, minute, 3, 2, and 3 mm, respectively, perhaps indicating the approach of a late August laying period. In addition to body molt, the birds showed the following flight feather replacement: three new primaries and one growing; five new primaries, two growing, two new, one growing and one dropped secondary, and three growing rectrices; primaries 1 and 2 new, third pair and one pair of secondaries growing; rectrices 2-5 and primaries 2 growing with primaries 1 new, secondaries L 1 and R 2 partly grown, R 1, new; rectrices 2-3, secondaries 8-9 and primaries 5 growing, primaries 1-4, new.

Chloroceryle americana. Green Kingfisher. A single female was taken 9 June (I). The largest ovum was only 2 mm, but the oviduct was greatly enlarged. She was replacing secondaries 10, many body feathers, and one pair of rectrices. Primary molt was more difficult to determine. Numbers 1-1 were growing though the left was nearly twice the length of the right. Primaries 2, 3, and 6 were not molting and showed no wear. Primaries 4, 10, and right 5 were old. Left 5 was new and about 1/10 grown. Primaries 7, 8, and left 9 appeared newly replaced. Right 9, not quite fully grown, retained a basal sheath.

Selenidera spectabilis. Yellow-eared Toucanet. Two toucanets were collected 3.2 km SE and 2.4 km S of Cariblanco. The male, taken 5 August, had a testis 10 × 5 mm and was in heavy body molt. In addition, one pair of rectrices, two pairs of primaries (3-4), and three pairs of secondaries (4, 9, 10) were growing. The female (15 August) also was molting but apparently was not breeding (follicle 1 mm).

Glyphorhynchus spirurus. Wedge-billed Wood-creeper. A single male (testis 9 × 6) was taken 6.4 km W Guápiles on 24 July. Rectrices 1 and primaries 3-4 were growing; primaries 1-2 were new. Ricklefs collected two specimens at the Osa Station on 7 and 10 May. The ovaries of both were small; both were molting flight feathers.

Dendrocolaptes certhia. Barred Woodcreeper. Two males (II: 23, 29 July) had testes of 12 and 16 × 10 mm, respectively. In addition to body molt in all areas, both were replacing rectrices 1, primaries 3-4, and secondaries 1. The former also was replacing secondaries 9. A female (ovarian follicle 2 mm), taken 27 July (II), exhibited light body molt and asymmetrical molt of two rectrices. Ricklefs collected a male and a female (IV) on 9 May. The female was not breeding; the male's testis was moderately enlarged at 11 × 8 mm. She was replacing primaries 1-2; he was replacing the central rectrices, primaries 2-3, and was in heavy body molt. Dickey and van Rossem (1938:322) collected a breeding pair in El Salvador on 30 July 1925. The female contained an oviducal egg. Both individuals were undergoing the

annual molt with "new feathers appearing everywhere on the body, wings, and tail."

Xiphorhynchus guttatus. Buff-throated Wood-creeper. Two females were taken at Jiménez on 10 and 15 May. The largest ovum of the former was 12 mm and of the latter, 1 mm, but neither was molting. A male from Los Diamantes (27 July) had a testis 9 × 7 mm and low to moderate numbers of body feathers growing or new. Primaries 1-2 were new, 3 fully grown with a basal sheath, and 4 half grown. Rectrices 1 also were growing.

Lepidocolaptes souleyetii. Streak-headed Wood-creeper. Of 14 adults collected (I, II, VI), 3 (24 May; 12, 18 July) were considered to be breeding but not molting, 3 to be molting but not breeding (13, 17, 17 August), and one neither molting nor breeding (23 July). One male in heavy body and flight feather molt had incompletely regressed testes (27 July, testis 6 × 3.5). The remaining six birds showed evidence of molt-breeding overlap. A single female (11 August) had a brood patch, a follicle of 3 × 2 mm, and was in early stages of molt (light dorsally and ventrally). One male (7 June), with a 15 × 7 mm testis (Stage 7), showed only light dorsal body molt. The other four males (10, 17 July; 13, 19 August) had testes of 10 × 7, 13, 19 × 11, and 10 × 7 mm. In addition to growing body feathers, they showed respectively: primaries 1-2 growing, 3 dropped, secondaries 8 dropped; primaries 3-4, secondaries 8, and rectrices 1 growing; secondaries 8 growing; primaries 4-5 growing.

Automolus ochrolaemus. Buff-throated Foliage-gleaner. A male replacing a moderate number of body feathers, rectrices 1, primaries 6 (1-5 new), and secondaries 2 was taken 26 July (II). The testis (9 × 4) probably was regressing, since a male taken on 9 May (IV) had a testis of 14 × 7 mm. It showed light body molt. A male and a female, taken 11 September at Finca Helechales, showed no molt or breeding.

Xenops minutus. Plain Xenops. Thirteen specimens were collected from five localities in Costa Rica (I, II, III, V, VII). Males, taken 19 and 29 April, had testes of 8 × 5 and 8 × 3 mm; the second bird was undergoing heavy body molt and growing primaries 3-4 (1-2 new). Another male (testis 8.5 × 4), taken 24 May, showed heavy body molt, primaries 1-6 new and 7 growing and secondaries 1 new, 2-8 growing, and 9 dropped. Five nonbreeding adults were taken from June through September. Only two were molting. A male, taken 26 August, not molting but in what appeared to be very new plumage, had a testis 6 × 5 mm, indicating incomplete regression during molt, or perhaps very rapid gonadal recrudescence after molt. Another nonmolting male, taken 27 November at Finca Jiménez, had a testis of 5 × 2 mm.

Thamnophilus bridgesi. Black-hooded Antshrike. Two adult females, collected at Finca Helechales, were just beginning the molt. One (3 September) had a yolked ovarian follicle of 15 mm; the other (7 September) had no enlarged ova. The former individual exhibited moderate replacement dorsally and ventrally, with many feathers completely ensheathed. The latter bird showed light body molt.

Myrmotherula schisticolor. Slaty Antwren. A breeding male (testis 8 × 5) from the Osa Station (7 May) was undergoing heavy molt of body feathers and secondaries. Two specimens, collected at Helechales on 12 and 13 September, were neither molting nor breeding.

Gymnopithys leucaspis. Bicolored Antbird. Both Bicolored Antbirds collected (II) were molting. The female (2 September) was not in breeding condition. The male (4 September) had a testis of 8 × 4 mm, and was replacing moderate numbers of body feathers and two pairs of rectrices.

Attila spadiceus. Bright-rumped Attila. Males, taken 12 May (I), 13 July (I), and 14 September (III), had testes of 12 × 4, 6, and 3 × 1.5 mm, respectively. None was molting. A fourth individual (27 June, I), with testes of 9 × 4 mm, was undergoing heavy body molt in all areas and growing primaries 1-2. The testis was in Stage 7 B.

Pachyramphus polychopterus. White-winged Becard. A male (testis 12 mm) and a female (largest ovum 4 mm) were taken on 15 and 9 July at Finca Jiménez. The male showed light but symmetrical ventral body molt.

Tityra semifasciata. Masked Tityra. Six males, taken (I) over a period of 3 months, all were in breeding condition with testes ranging from 10 × 5 to 13 mm in length. Only one (19 June) was not molting. Specimens from 13, 27 July and 16 August, apparently initiating molt, showed light to moderate replacement of body feathers; others from 13 July and 13 August were growing primaries 1-2; in the latter individual secondaries 8 were dropped as well.

Tityra inquisitor. Black-crowned Tityra. A male and a female, collected 25 and 26 April, both exhibited a light body molt. The female was not breeding. The male had a testis of 7 × 4 mm, in Stage 7.

Querula purpurata. Purple-throated Fruitcrow. The 7 × 4 testes of a male, taken (II) 28 July, probably were below breeding level for a bird of this size. However, testes size indicates either incomplete regression, or, since the molt was well advanced (primaries 7-8, secondaries 2, 7, 9, rectrices 2-4, and large numbers of body feathers growing), at least partial overlap of molt and breeding.

Chiroxiphia linearis. Long-tailed Manakin. I have examined the gonads of more than 100 members of this species, many microscopically. Molt-breeding overlap does occur in some individuals and will be considered in detail elsewhere (Foster, unpubl. data).

Megarhynchus pitangua. Boat-billed Flycatcher. Five flycatchers were collected at Finca Jiménez. A male, taken 25 April, had a testis of 13 × 6 mm (Stage 7) and was in heavy body molt including the replacement of wing and tail coverts. A paired male (testis 15 × 8) and female (follicle 2 mm), taken 12 August, both were growing numerous body feathers and one pair of rectrices. The male was growing one pair of primaries and two pairs of secondaries, the female, two pairs of primaries and three pairs of secondaries. A male (testis 14 × 7 mm), taken 14 August, was not molting.

Myiodynastes maculatus. Streaked Flycatcher. A male with a 15 mm testis was collected 13 July at Finca Jiménez. It was molting lightly to moderately in all tracts. A molting female, taken 17 August, was not breeding.

Pitangus sulphuratus. Great Kiskadee. Three females, collected on 8 (I), 23 (II), and 27 (II) July, showed no reproductive activity. The label of one (27th) indicated molt, though the extent was not noted, and the bird was skeletonized. The three males, taken at Los Diamantes (25-two, 28 July), had testes of 11 × 4, 7 × 3, and 8 × 3 mm. The testes of the latter two birds probably were incompletely regressed. Both were in moderate body molt. The latter one also

was growing one pair each of primaries and secondaries. The male with the largest testis showed no evidence of molt.

Terenotriccus erythrurus. Ruddy-tailed Flycatcher. A male, collected on 10 May (IV), had a testis of 5 × 3.5 mm. Primaries 5 were growing, and there was light body molt. A male (testis 7 × 4 mm), taken 29 July (II), was replacing numerous body feathers, two pairs of secondaries, and four pairs of primaries.

Oncostoma cinereigulare. Northern Bentbill. The testes in males of this species apparently show considerable variation in breeding size. A nonmolting male, collected (I) 9 May, had a testis 11 × 5 mm and was assumed to be breeding. However, the 6 × 4 mm testis of a male, collected (I) 8 June, showed numerous developing sperm and sperm free in the tubule lumina. This male was growing four pairs of rectrices; the fifth pair had dropped. One pair of secondaries had been replaced; three pairs were growing. Three pairs of primaries were new, and two pairs were growing along with large numbers of body feathers. Another male whose testis was of apparent breeding size (I, 15 July, 8 mm) was replacing large numbers of body feathers, three pairs of secondaries, and two pairs of primaries. Other specimens showed no overlap.

Myiopagis viridicata. Greenish Elaenia. Two adult females, taken (I) 25 April and 15 May, had follicles of 1.5 and 3.0 mm. The latter had a greatly enlarged oviduct. Both showed light to moderate molt. The latter also was replacing the upper-tail coverts. Nonbreeding females (I, 13 and 17 August) were replacing body and flight feathers. The single male collected (I, 13 August) had a testis 7 × 5 mm and showed heavy body molt and growing primaries 1 and 2.

Microcerculus marginatus. Nightingale Wren. A male and a female were taken on 2 September at Finca Helechales. The male had a testis of 8 × 6 mm and was growing many body feathers, two pairs of primaries, and one pair of secondaries. The female was neither breeding nor molting.

Ramphocaenus melanurus. Long-billed Gnatwren. A female, taken (I) 19 May, had a greatly distended oviduct indicating recent egg-laying. She was undergoing a light body molt. A male, taken (I) 30 May, exhibited moderate to heavy dorsal body molt but was not breeding (testis 2 × 1). Males from Tesalia (5 July) and Diamantes (23 July) with testes of 7 × 4 and 5 mm showed light body molt. Rectrices 6 also were missing from the latter specimen.

Hylophilus minor. Lesser Greenlet. Three males, taken at Finca Jiménez (11, 12 and 17 August), had testes of 3 × 2, 7 × 5, and 6 × 5 mm. The first was renewing primaries 1-3 and secondaries 8-9, the last, only primaries 1-3. Both were growing a number of body feathers. The male with the largest testis exhibited light ventral body molt. A nonmolting, nonbreeding female was taken 2 May.

Cacicus uropygialis. Scarlet-rumped Cacique. Male and female Scarlet-rumped Caciques (testis 10 × 8; largest ovum 9 × 9), taken 24 July in the Río Toro Amarillo forest, were breeding but not molting. However, another male, taken at nearby Los Diamantes a few days later (27 July), had a testis 9 × 6 mm and was molting a moderate number of body feathers and one pair each of primaries and secondaries.

Sturnella magna. Eastern Meadowlark. A heavily molting male, with a Stage 7, 10 × 5 mm testis, was

taken 27 August (I). In addition to body feathers, it was replacing the first three pairs of primaries.

Basileuterus rivularis. River Warbler. A male from near Cariblanco (3 August) had a testis 5 × 3 mm and was replacing light to moderate numbers of body feathers in all areas. Primaries 1 were two-thirds grown, and primaries 2, half grown.

Cyanerpes cyaneus. Red-legged Honeycreeper. Fourteen specimens were collected between 25 April and 17 August. All adults but one were breeding. Only a single female (25 April) showed evidence of overlap. She had a yolked ovarian follicle (8 mm) and was replacing the upper tail coverts and moderate numbers of body feathers.

Euphonia gouldi. Olive-backed Euphonia. A male from El Silencio (22 June) with a 6 mm testis was not molting. Another male, from Los Diamantes (29 July), had a testis of 5 × 3 mm and was replacing body feathers, tail coverts, and one pair of secondaries.

Tangara gyrola. Bay-headed Tanager. Breeding males, collected at Helechales on 2 and 4 September, with testes of apparent breeding size (8 × 5, 8 × 5), exhibited light body molt and moderate body molt with one pair of secondaries growing, respectively. Males, collected there on 4 and 15 September with testes under breeding size (5 × 2, 5 × 3), exhibited moderate body molt only.

Tangara lavinia. Rufous-winged Tanager. A male and a female were shot from a small flock on 2 July at El Silencio. The female, whose largest follicle was only 1 mm, showed light body molt. The male had a testis 8 mm long and was replacing large numbers of body feathers, two pairs of primaries (4-5), and one pair of secondaries (8).

Thraupis episcopus. Blue-gray Tanager. A pair was collected at Finca Jiménez on 31 August. Though they were obviously breeding (largest ovum 9 mm, yellow-orange; testis 10 × 8 mm), both were molting. The female was growing two pairs of primaries and a moderate number of body feathers. Secondary molt may have been interrupted; secondaries 1-6 were new; 7-9 appeared old. The male was replacing many body feathers, one pair of rectrices, and three secondaries on one side only. Symmetric molt of the primaries had progressed to number 5 which was partly grown. A male from El Silencio (1 July) was breeding (testis 11) but not molting. Another from Los Diamantes (28 July) had a testis below breeding size (6 × 4) and was molting.

Ramphocelus passerinii. Scarlet-rumped Tanager. Three adults were taken near Tesalia and six at Los Diamantes. Three males (10, 23, 26 July) were molting but not breeding (testes 1 × 1 to 4 × 2). Four males (8, 25, 27, 27 July) apparently were breeding (testes 11 × 7 to 9 × 7) but not molting. One (28 July) had a testis 9 × 6 mm and showed moderate molt. A female (9 July) with a 1.5-mm ovarian follicle exhibited moderate body molt and was growing primaries 1.

Tachyphonus rufus. White-lined Tanager. A male, taken on 28 July (II), had a testis of 8 × 5 mm and exhibited light body molt dorsally and ventrally.

Arremonops rufivirgatus. Olive Sparrow. A pair, taken (I) 30 May, were in breeding condition. The nonmolting female (largest ovum 1 mm) had an active brood patch, the male, a testis 6 × 6 in Stage 7. The male was replacing a moderate number of body feathers. Other adults collected (I: 3 May, 13, 15 August) were not molting (testis 4.5 × 3.5 and 7 × 5; largest ovum 2 mm).

ANALYSIS OF SPECIES

Payne (1969b) divided the birds on which he reported into four categories. The first includes those replacing feathers that he considered to have been lost accidentally. Though some individuals were growing as many as hundreds of body feathers, none was replacing flight feathers. On the other hand, I have considered replacement of body feathers in the absence of flight feathers to be a normal molt especially since the molt cycles of tropical species are not well known. It has been shown for several species that the percentage of any population undergoing a prenuptial molt (i.e., the molt most likely to involve only body feathers) may vary considerably (Davis 1971, Foster 1967). Thus, not all individuals necessarily would be molting. I do not assign any of the species considered in this paper to this category. The only species in which loss may have been adventitious are *Tityra inquisitor*, *Ramphocaenus melanurus*, and *Tachyphonus rufus*, but only because their body molt is designated as light. This is not really a valid criterion since molt may begin and/or end with few feathers. In addition, when it overlaps breeding, molt may be considerably protracted (Snow and Snow 1964) by means of a decrease in the number of feathers growing at any one time or in their rate of growth (Newton 1966). Also of interest is the inclusion by Payne (1969b) of several cuckoos and cuckooshrikes in this category. He attributes their extensive adventitious loss to the thinness of their skin. My experience with neotropical cuckoos and trogons, many of which have equally thin skin, does not support this. I have collected more than 30 individuals of these two groups, and none showed feather replacement that was not clearly attributable to molt. It is also difficult to see how large numbers of feathers could be lost accidentally from several or all parts of the body symmetrically and simultaneously. Feathers of the back and rump are easily shed in cuckooshrikes and perhaps trogons and pigeons (Thomson 1964). This does not explain the molt data for most individuals considered here, however, since they were molting extensively in other areas as well.

Another category of Payne (1969b) includes birds in which the molt has been interrupted by breeding. The only specimen I collected that I suspect to have shown this is a female *Thraupis episcopus*. However, this phenomenon has been reported for several other neotropical species (e.g., Miller 1961, 1963, Snow and Snow 1964, Snow 1966).

Crotophaga sulcirostris, *Trogon massena*, *Selenidera spectabilis*, *Xiphorhynchus guttatus*, *Automolus ochrolaemus*, *Querula purpurata*, *Pitangus sulphuratus*, *Hylophilus minor*, *Basileuterus rivularis*, and *Euphonia gouldi* probably all belong to Payne's third category. In molting individuals of this group, the gonads are incompletely developed or incompletely regressed. I place all of the other 37 species in the fourth category of true molt-breeding overlap. However, certain individuals of these species exhibit overlap due to incompleted development or partial regression and thus qualify for category 3. In fact, I believe that these two categories represent a continuum. In some species, 30–40% of the molt occurs when the testes are at full size. The gonads may decrease in size during the middle of the molt and increase again toward the end (Miller 1961, Wolf 1969), or they may regress during the terminal stages only (King 1972b). This may indicate some metabolic incompatibility between molt and breeding in certain species at certain times. Incomplete regression decreases the amounts of energy and nutrients required for the rebuilding of the gonads and perhaps also allows enough hormone to be produced to maintain territoriality, dominance, or other similar hormonally associated activities. In other species, molt and breeding overlap completely.

The extent of the molt in breeding individuals may vary considerably (Payne 1969b). Several birds reported here showed light body molt only. Others were replacing hundreds of body feathers in addition to primaries, secondaries, and rectrices.

FREQUENCY OF OVERLAP

Of the 960 individuals considered, 95 or approximately 10% showed evidence of molt-breeding overlap. If those in which the molt could have been adventitious (five) are eliminated, the percentage drops to 9.4; if all individuals in those species where overlap does not include flight-feather molt are eliminated, the percentage falls to 8.1. This still is considerably higher ($P < 0.05$) than the percentage found by Payne (1969b, 41 of 1050 = 3.9%) for specimens in his four categories combined. Moreau (1936) found 117 of 2811 specimens or 4.2% to exhibit some overlap ($P < 0.10$). It should be recalled, however, that many individuals considered in these three studies probably were taken outside the breeding and molting periods of their species, and thus these percentages are biased downward.

In addition, the species reported usually

were not collected in equal numbers. Thus it is probably more meaningful to examine the percentage of species rather than individuals showing overlap. Forty-seven, or 20.2% of the 233 species I considered showed overlap; 12.6% ($P < 0.05$) of Payne's (1969b) species and 13.5% ($P < 0.10$) of Moreau's (1936) showed overlap. Approximately 8.0% ($P < 0.05$) of the species combined from Miller's studies (1954, 1961, 1963) showed overlap, although his collections included a sizeable number of temperate migrants which biases the percentage downward. Again, many species were not collected during their molt or breeding periods.

Other authors have described molt-breeding overlap in additional tropical species although data are not expressed as percentages of specimens or species examined. Included are African, neotropical, and southeast Asian forms. Because the references to these species are widely scattered and sometimes obscure, it is of value to note them here. Species reported to exhibit overlap are listed in the appendix with the source of the information. On the basis of data reported here and information in the literature, 121 tropical species (excluding all Australian arid region birds) have been noted to exhibit molt-breeding overlap. Data for 63 of these species were taken at least in part from females with enlarged ova or from males or females for which additional information other than gonad size indicated breeding. Data for the remaining 58 were taken either from males with enlarged testes or from specimens for which sex and criteria used to determine breeding were not specified by the investigator. Undoubtedly, published accounts of other species with overlap have been missed and future studies will reveal its existence in additional forms; nevertheless, the figure is a generous one for it includes species that exhibit interrupted molt as well as many for which the data are extremely limited. I believe, however, that enough evidence exists to assume that overlap is a real phenomenon in most of the species considered here and of regular occurrence in tropical areas.

DISTRIBUTION OF OVERLAP

Eventually, when molt-breeding overlap is studied in a systematic manner drawing equally on samples of birds from all phylogenetic groups, geographic areas, and ecological types, a detailed examination of the relationship between overlap and such parameters will be important. Samples presently available allow us to consider such relationships only in the most general way. This was done on the basis of information summarized from local field guides, annotated checklists, and area faunas (e.g., Haverschmidt 1968, Mackworth-Praed and Grant 1970), from life history works (e.g., Skutch 1969), and from papers dealing with particular species (e.g., Feduccia 1970, Jenni and Collier 1972), as well as my own data.

The number of species showing overlap seems to vary to some degree with both geography and phylogeny. Forty-eight species are from Africa, 72 from Latin America, and 1 from Asia. Overlap also has been reported in a number of Australian species, though these perhaps represent a unique case and are not considered here. Interestingly, overlap has rarely been reported among Indian and Asian forms, perhaps because of a paucity of information about avian molt and breeding cycles in these areas. Those instances which have been noted most often are confined to the period of postfledging dependency (Ward 1969, Fogden 1972). Overlap also seems to be more prevalent among certain families and genera, for example, the Columbidae, Cuculidae, and Thraupidae, particularly the genus *Tangara*.

Molt-breeding overlap shows no obvious correlation with food preference of the adult. Though many of the species exhibit wide latitude in feeding habits, 47 of the 121 species were considered to be primarily insectivorous, 33 primarily frugivorous, 24 granivorous, 13 omnivorous, 3 nectarivorous, and 1 piscivorous. Food type of the parent might be expected to be of little significance since a majority of nestling birds probably are fed insects. However, different bill adaptations in the adults may affect their ability to gather insects for their young.

It also appears that little relationship exists between overlap and habitat type. Of the 94 species for which some information was obtained, 28 are found in heavy forest or woodland, 32 in thinned woodland, forest edge, or semi-open areas, 28 in open or cultivated areas, 2 in all areas, and 3 in very specialized habitats.

Perhaps of greatest interest will be the relationship between reproductive biology and molt-breeding overlap. Unfortunately, this aspect of the life history of most of the species is very poorly known, and no relationships can be determined at present. The extremely limited data available can be summarized as follows: at least 16 of the species breed year-round. Five of the species are paired year-

round. Twelve species are parasitic. At least 19 nest in holes or tunnels, often (8 species) using natural cavities without further modification. Monogamy is suggested for 31 of the species, polyandry for 2, polygamy and promiscuity for 1 each. Mean clutch size, based on ranges given in the literature, is small, at 2.5 approximately.

Unfortunately, with regard to each of these variables, no standard exists against which the proportions of each type may be compared.

DISCUSSION

The source of energy and specific nutrients necessary for molt during breeding probably varies with different species, but several general categories may be outlined. Some species utilize food sources that are extremely abundant for a very short period and so limited at other times that both molt and breeding must be completed during this period of superabundance. If this period is short enough, the two activities must occur simultaneously. Possibly, birds exhibiting overlap for this reason assimilate energy and nutrients into reproduction at a maximal rate. Thus resources used for molt would not be taken from reproduction. Alternatively, overlap may result in a reduction of resources devoted to breeding. Overlap still may be advantageous, however, if it allows molt to shift from a period of food scarcity to one of food abundance. If food resources of lean periods limit population size, then the shift may increase the carrying capacity of the environment. Under certain circumstances, selection may favor adaptations which increase carrying capacity, even if they do so at the expense of the reproductive rate (Cody 1966, 1971).

The second category includes birds in which particular resources for reproduction are critical only for a brief part of the nesting cycle, and whose food supply is reasonably uniform throughout most of the reproductive period of the species. Prenuptial molt can occur simultaneously with the earlier stages of reproduction and postnuptial molt with the later stages, or a single molt can span reproduction but be interrupted when resource demands reach critical proportions. Thus, the amount of reproduction is limited by energy or nutrient availability or ability of the parents to provide a limited resource over some finite period in the cycle. During this period, all of the available resource is channeled into reproduction. To devote excess energy and nutrients during some other part of the reproductive period to nonreproductive activi-

ties such as molt is not selectively disadvantageous as long as these activities in no way interfere with reproduction. This probably is a pattern commonly associated with molt-breeding overlap. For example, Snow and Snow (1964) found great constancy in the timing of molt from year to year in several species. Even in those species with a continuous or nearly continuous breeding season, the majority have a well-defined molt period adhered to by most individuals of the species. On the other hand, breeding often is timed by the onset of the rains or of some other environmental factor whose date of initiation may vary as much as a month or occasionally more from year to year. Thus, if the postnuptial-molt period is fixed to a particular part of the calendar, the ability to overlap molting and breeding may be significant in allowing for second broods or renesting in those years when the environmental trigger for breeding is "late." It would also allow individuals to begin breeding as soon as favorable conditions arose, even in years when the environmental trigger was "early" and the birds were still in prenuptial molt.

Finally, one may explain overlap of molt and breeding in some species through a reduction in energy or specific nutrients required for molt and/or breeding so that enough are available for both activities to occur simultaneuosly. I have no data to suggest any reduction in resource requirements for molt. Perhaps some adjustment could be made in order to reduce energy expended on thermoregulation. The timing of the molt to coincide with highest environmental temperatures may serve this purpose in some species (Mewaldt 1958, Middleton 1969).

Reproductive costs may be reduced in a variety of ways. For example, several species exhibiting molt-breeding overlap are parasitic. Others, of various families, occupy old nests (especially those built by other species), or natural cavities that they use without modification. In addition, the majority of the overlap species for which data are available have clutch sizes smaller than those characteristic of the temperate members of their species, genus, or family (Moreau 1944, Lack 1947, Skutch 1949, 1967a, Lack and Moreau 1965, etc.).

As Ricklefs (1968) noted, if selection maximizes the number of young reared, then "the energy required of a brood of young ideally should match exactly the maximum food gathering rate of the adults at some critical period when the rate of energy utilization is

greatest. Any genotype that wastes potentially available energy will be at a competitive disadvantage." This applies equally to extra energy available from a reduction in clutch size, from parasitic habit, from the use of old nests, or from any other trait that reduces the energy devoted to some necessary activity during the reproductive period. Presumably, selection should favor the shunting of this extra available energy into some other aspect of reproduction.

Because nestling birds are highly vulnerable to predators, the use of extra resources (energy or specific nutrients) to increase the growth rate of the young birds and therefore to decrease their time of vulnerability in the nest would seem advantageous. However, birds in nature probably grow at maximum rates and thus can adjust growth rates only by decreasing them (Ricklefs 1969). If a slower growth rate reduces the requirement of each young sufficiently, then the parents may be able to feed another young. But, the requisite decrease in growth rate could be physiologically impossible in some species. Also, if a third young is added, predation may increase with the slower growth rate and added conspicuousness of nests to predators which apparently increases with clutch size (Skutch 1949, Snow 1970).

In some species, molt-breeding overlap itself, by prolonging the potential breeding season of an individual, can increase the probability that the individual will produce offspring (Foster 1974). In areas of high nest predation and low nest success, such as the tropics, this may be very important.

Also of interest to a discussion of molt-breeding overlap are the physiological mechanisms controlling the onset of each event. Though the mechanism triggering molt has not been determined definitively for any species, it has been suggested that molt and breeding are mutually exclusive events and that the hormones stimulating each are antagonistic to the onset of the other. For example, in most species the annual molt follows breeding or, as in several tropical forms, the timing of breeding may be controlled by the timing of molt (Miller 1962, Snow and Snow 1964). However, the data reviewed here indicate that mutual exclusion and antagonism do not operate in all instances. In addition, it has been shown (Kobayashi 1958, Thapliyal 1969) that the degree of correlation between onset of molt or breeding and levels of various hormones may vary considerably in different species. In many species, particularly those that exhibit overlap, it appears that breeding and molt are timed independently according to appropriate environmental signals (Payne 1972). Physiological mechanisms triggering molt or breeding, though influenced by the progress of the other event, are independent of it (Wolfson 1954, Lofts and Murton 1968).

SUMMARY

New data on the overlap of molting and breeding in 47 neotropical species are presented. Seventy-four other tropical species also are reported in the literature to show this phenomenon. Resources necessary for molt during breeding may come from a reduction in those devoted to reproduction or from excesses available during certain parts of the reproductive period. Molt-breeding overlap may be important in increasing the efficiency with which a species uses its environment. It may provide increased opportunities for renesting in certain circumstances.

ACKNOWLEDGMENTS

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APPENDIX. Species reported in the literature[a] to show molt-breeding overlap.

Species	References[b]
Gallinula chloropus	11
Pterocles burchelli	11
Streptopelia semitorquata	11
Scardefella inca	3
Leptotila verreauxi	3
Oreopelia albifacies	3
Geotrygon frenata	6
Clamator glandarius	11
C. jacobinus	11
C. cafer	11
Cuculus canorus	11
Chrysococcyx klaas	11
C. caprius	11
Crotophaga ani	14
Geococcyx velox	3
Steatornis caripensis	12
Amazilia franciae	6
Colius striatus	7, 10
C. colius	11
Upupa epops	1
Lophoceros alboterminatus	8, 9

APPENDIX. *Continued.*

Species	References[b]
L. bradfieldi	9
L. pallidirostris	8, 9
L. nasutus	8, 9
L. erythrorhynchus	8, 9
L. flavirostris	8, 9
L. deckeni	8, 9
Berenicornis albo-cristatus	8, 9
Bycanistes bucinator	8, 9
B. cylindricus	8, 9
B. subcylindricus	8, 9
B. brevis	9
Ceratogymna atrata	8, 9
Trachyphonus darnaudii	11
Indicator minor	11
I. variegatus	11
Geocolaptes olivaceous	11
Xiphorhynchus triangularis	6
Synallaxis albescens	4
Thamnophilus doliatus	14
Pipreola riefferii	6
Tyrannus melancholicus	4
Atticora cyanoleuca	6
Coracina caesia	11
Campephaga phoenicea	11
Pycnonotus xanthopygos	10
P. barbatus	2
P. goiavier	15
Andropadus latirostris	2
Phyllastrephus flavistriatus	10
P. fischeri	11
Thryothorus genibarbus	6
Melaenornis edioloides	11
Turdoides jardineii	7
Cinnyris reichenowi	1
Hylophilus flavipes	4
Tangara arthus	6
T. xanthocephala	6
T. labradorides	6
Zonotrichia capensis	5, 16
Aimophila ruficauda	3
Geospiza fortis	13
G. fuliginosa	13
G. scandens	13
Camarhynchus crassirostris	13
Lagonosticta jamesoni	11
Amadina fasciata	11
Hypochera amauropteryx	11
Vidua nigerrima	11
V. macroura	11
V. paradisaea	11
Bulbalornis albirostris	11
Petronia xanthosterna	11
Sporopipes squamifrons	11