Patterns in the Calling Activity of the Pauraque Nightjar, *Nyctidromus albicollis*

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The Pauraque, *Nyctidromus albicollis*, is a very vocal nightjar with a varied repertory of sounds. I have heard five distinctly different calls that are common and two others that are not common. The common ones are: 1. A loud, far-carrying whistle that I now render as *to-wee-oo*; 2. a soft *uh-wup, uh-wup, uh-wup, uh-wup-per-ah* that is variable in the number of preliminary *uh-wups* and may have none; 3. a soft but sharp *wut* or *wit*, usually repeated two or three times; 4. a drumming sound, *thun-thun-thun-thun...* (or *thack-thack-thack...*) that is soft, low and sustained for many seconds and 5. a "growl". I have once heard a sound I would render as *waa-oo* and again once a low, soft drawn-out *woooo*.

As is to be expected, the sounds are used in different situations. The first call seems to be a declaration of territorial ownership, but additional uses are discussed later. The second call seems to be used for communication between members of a pair or family group. The third call seems to be an alarm. The fourth call accompanies a ritualized display that I interpret as courtship. The fifth call I have heard only mixed with other calls and its use is not at all clear.

This paper mainly concerns the first call.

Methods

In December 1983 I began a study of the frequency of calls 1 and 2 by counting the number of calls in a five-minute period at 1 hr, 1 1/2 hr, 2 hr, 3 hr and 4 hr after sunset on as many days as possible in each month. The study lasted until the end of June 1984 when calling had ceased. The results were plotted but gave no clear picture, so the method was altered for the two subsequent seasons 1984-1985 and 1985-1986.

On at least two nights per week, as I sat at my desk working, I would listen for the calls of the Pauraque. I could hear up to four different birds calling at the same time and I would record the time when a bout of calling began and when it ceased. Both calls 1 and 2 were noted, but whereas the first was often repeated continually for many minutes the second was always isolated or repeated only once or twice. In the analysis only call 1 was used.

The start of the bout of calling was always easy to notice, and once calling had begun, I would check my watch every 10 - 15 min. However, the end was not always easy to notice because the calls sometimes got softer towards the end of a long bout, and also because my attention would be distracted from the calls by the other work I was doing. If I realized that calling had stopped without my being sure of the time, I took the time of the stoppage as the time half way between noticing the absence of calls and the time at the last check of the watch. Any error here is a systematic error affecting all observations to a greater or lesser degree and does not affect the conclusions that can be drawn.

Table 1 Dates for the end and start of calling activity 1985 - 1992; call 1 only. The day of the lunar cycle is given in brackets, day 1 being new moon.

Last Call	First Call	No. days between dates
6.VI.85 (D19)	21.X.85 (D8)	138
10.VI.86 (D4)	15.IX.86 (D12)	97
21.VI.87 (D25)	9.VIII.87 (D16)	49
27.VI.88 (D14)	20.VIII.88 (D9)	54
22.VI.89 (D20)	15.IX.89 (D16)	85
6.VI.90 (D14)	25.IX.90 (D7)	111
< 12.VI.91 (D1)	26.IX.91 (D19)	106
21.V.92 (D20)	7.IX.92 (D5)	109

Only the period from sunset to midnight is covered. During periods of moonlight, calling goes on after midnight, and probably all night during the few days around full moon, at least during the months February - May. Sporadic observations were made in the period from midnight to sunrise and the methods used in treating these observations are given when they are dealt with in the next section.

All the observations were made at Haven Hill Farm on Leotaud Trace near Talparo.

Results

Annual Pattern:

With the onset of the rainy season calling ceases (Table I). Calling begins again in August with the *wup-per-ah* call but the *to-wee-oo* call may be delayed several weeks (Table I). In all years from 1985 to 1992 calling has ceased in late May or June. The resumption of the *to-wee-oo call*, however, is spread out over a much longer period, from August to October. This may be attributed to the fact that the start of calling may be only a single call which may not be repeated for another month. Perhaps where the beginning is late I may have missed an earlier call, but weather may be an influence as well. It should be noted that whereas the cessation of calling is spread over many days of the lunar cycle the resumption of calling has always fallen between Day 5 and Day 19 of the lunar

cycle i.e. from near first quarter to just after full moon (Table I).

In the study from Dec. 1983 to June 1984 when counts were made in the specified 5-min intervals (see Methods) the only pattern that emerged on analysis was an annual pattern (Table II). Fom a low frequency in Dec. 1983 calls increased up to March 1984 and thereafter declined.

For both the other seasons the number of minutes spent in calling and the number of minutes spent in observation per month were determined (Table III). In 1985 the peak rate of calling (minutes of calling as a percent of minutes of observation) occurred in February whereas in 1986 the peak came in March. It is clear that for every season the rate of calling was low when calling began, increased up to February or March and thereafter remained high until May. Calling always ceased with the arrival of the rainy season.

Lunar pattern

On the record sheets for the seasons 1984-85 and 1985-86 the day of the lunar cycle was written in against each observation with new moon as Day 1. Then a table was prepared for each season's record giving for each observation in chronological order the following items: the day of the lunar cycle, the number of minutes of calling, and the number of minutes spent in observation. From these two tables (one for each of the two seasons) another table was prepared from the pooled results by rearranging the material to give under each day of the lunar cycle the number of minutes spent in calling and the number of minutes spent in observation. The percentage of observation time spent in calling was then determined for each day and the figures plotted as a histogram (Fig. 1).

The figure shows that the percentage of time spent in calling increases from Day 1 to about Day 5 and then changes less noticeable up to Day 18, two days after full moon. There is then a dramatic drop to a low level until Day 28 when the percentage rises again. Thus, the pattern is not symmetrical about Day 16; there is

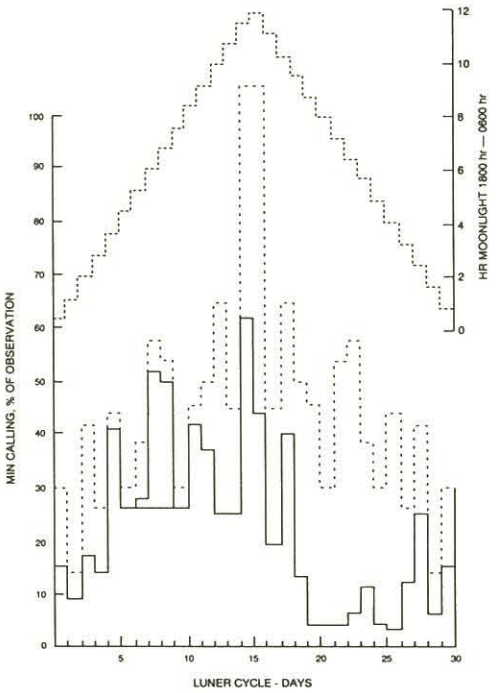

Fig. 1 The influence of moonlight on calling activity. The solid line, derived from the observations, shows that the amount of time spent in calling between 1800 hrs and midnight increases as the moon waxes and then drop off sharply four days after full moon. Adding a mirror image of itself to this histogram in order to take account of calling between midnight and 0600 hrs gives a symmetrical histogram (dashed line) which is similar to that for the number of hours for which the moon is visible from 1800 hrs to 0600 hrs over the lunar cycle (dotted line).

Table II Annual pattern of calling - Dec . 1983 - June 1984 Total number of calls per month obtained by adding all counts in the 5-min. observation periods (see text).

Month	No. calls	No. 5-min. periods	Calls/period
Dec.	433	26	16.65
Jan.	831	38	21.87
Feb.	1101	34	32.38
Mar.	2464	39	63.18
Apr.	1470	24	61.25
May	730	28	26.07
June	462	15	30.80
July	0	49	0

Table III Annual pattern of calling activity for the two seasons 1984-85 and 1985-86

Month	1984-85 Min. calling	Min. observ.	calls/obs X100	Min calling	1985-86 Min. observ.	calls/obs X100
Oct	49	1080	4.54	166	1890	8.78
Nov	181	1181	15.53	63	2940	2.14
Dec	372	3035	12.26	111	3630	3.06
Jan	618	4340	14.24	215	3175	6.77
Feb	877	2710	32.36	1183	3815	31.01
Mar	883	3410	25.89	1298	2640	49.17
Apr	735	2345	31.34	1474	3480	42.36
May	773	2485	31.11	1962	5225	37.55
June	82	1080	7.41	34	1255	2.71
July				0	2528	0

markedly less calling in the nights after Day 16 than before.

Most probably, the reason for this lies in the fact that the observations were restricted to the period between 1800 hr and midnight and that moonlight varies over this period from less than 1 hr at Day 1 to 6 hr at day 16, with no moonlight at all from Day 24 to Day 30., Therefore, if moonlight stimulates the birds to call, a great diminution in calling after about Day 20 can be expected. This is exactly what appears in Fig. 1. If results were available for the period midnight to 0600 hr then the figure might well be symmetrical.

If moonlight were as important in the period after midnight as it is in the period before, we would expect the pattern of calls in the period after midnight to be a mirror image of the pattern shown in Fig. 1 for calls before midnight. I tried to find evidence for this from my notes. They contain seventy observations for the period midnight - 0600 hr, thirty three of which are notes of calling in progress at a particular time, and another two of no calling at a particular time. The others refer to observations over several minutes with one as long as two hours.

To treat all of these observations in a uniform way (as though single observations at a particular time) the period after midnight was divided into six 1 hr periods and any observation of continuous calling over more than 1 hr or for less than one hour but spanning parts of two 1 hr periods was considered as two observations. The 2 hr period of calling that spanned 1 hr and parts of two others was considered as three observations. Continuous observation where there was no calling was similarly treated. Two or more periods of continuous calling within an hour were considered as one observation and an observation of calling on the hour was referred to the period ending with that hour. All the observations were then entered into a table, Table IV. The regular numerals refer to the observations with calls, the bold numerals to the observations without calls. Indicated in the table too are the periods when the moon is visible and when it is not. These are approximate only and were obtained by assuming that sunrise and sunset occurred at 0600 hr and 1800 hr respectively, that the new moon occurred at 0600 hr on Day 1 of the lunar cycle and that the moon rose 48 min. later each day.

As the table shows, there was calling in 40 out of 47 observations that were made during periods of greater or lesser moonlight and in 17 out of 23 observations that were made when there was no moonlight. If calling occurs regularly in the hour before sunrise as it does in the hour after sunset we should expect it on all or nearly all days. Unfortunately, there were no observations at this time from Day 10 to Day 23 inclusive so that this probability is not tested. However, there were exactly the same number of observations of calling in this 1 hr period (eleven) during the dark half of the lunar cycle as during the light half. Omitting these observations and the one observation with no calls as possibly biasing the results because of sunlight, we are left with calling in 6 out of 12 observations in the dark phase (50%) and 29 out of 35 in the light phase (83%). It would seem therefore that the results, though based on few observations, support the thesis that moonlight influences the number of calls in the six hours after midnight just as it does in the six hours before midnight.

In this period (midnight-dawn) there is no moonlight from Day 1 to Day 8. Moonlight increases from 48 min on Day 9 to 6 hr on Day 16 and after D 23 steadily declines to 48 min. near dawn on Day 30. This pattern is the mirror image of the pattern for the period 1800 hr - 2400 hr. and we would expect the pattern of calls to be a mirror image too. If we accept this and add a mirror image pattern to the pattern shown by the solid lines of Fig. 1 we get the symmetrical pattern of the dashed lines which is much the same as the pattern for the variation in the amount of time for which the moon is visible, the dotted lines of Fig. 1. This analysis leaves out of consideration the effect of light intensity on the frequency of calling. In clear skies light intensity would peak at Day 16 and fall off on either side like the graph

Table IV Distribution of nightjar bouts of calling in the hours after midnight over the lunar month. Regular numerals refer to the number of observations when calls were heard during each hour from midnight to 0600 hr. Bold numerals refer to the number of observations with no calls. There is only one entry per hour on any one day. Any observation on the hour was counted for the predceeding hour. The shaded areas designate the nights when the moon was not visible (See text).

Day:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Hr																														
1	12		1	11		1	1	1			1	1	2		1	21		1	4	1		2	1	11					1	
2												1										1	1	1						
3																1														
4																2			1	1			1	1	1					
5	1												1												1		1	1	1	
6	1	2		3		2	1	1	1															1	21	1	2	1	4	

for duration of moonlight. It is reasonable to expect that it too affects calling.

Daily Pattern

From the observations over the two seasons 1984-1985 and 1985-1986 those that covered the full six hours from 1800 hr to midnight were selected and are presented in Fig. 2. Several points should be noted.

1. There is no daily pattern in the sense that calling is restricted to a certain period of the night that is the same from night to night; the time during which calling occurs varies and so does the duration of calling.

2. As mentioned in an earlier study (Quesnel 1990), even if no calling occurs in the rest of the night it often occurs within an hour of sunset. There are 22 instances of this in Fig. 2.

3. On the other hand, there are very few cases (4) where there is no calling early in the evening when there is calling late at night. However, if the period between midnight and 0600 hr is considered as well, there are likely to be many more nights when calling occurs late i.e. after midnight and near dawn, although it has not occured at sunset. These nights would occur between full moon and the new moon.

Fig. 2

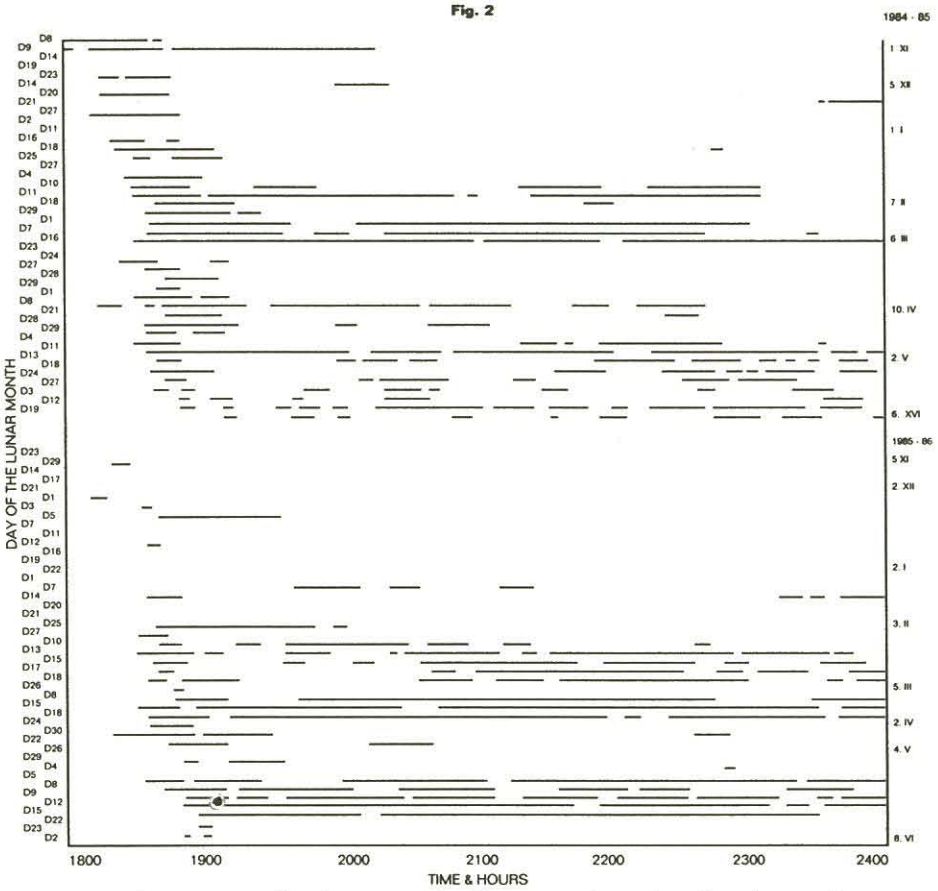

Fig. 2 Variation in the duration of calling on selected nights during the two seasons 1984 - 85 and 1985 - 86. The nights selected are those where observation was continuous from 1800 hrs. to midnight

4. In the early part of the season calling tends to occur in periods of shortened duration that are less fequent than those later in the season. From about February, spells of calling increase in duration.

5. Apart from the hour after sunset and that before dawn, calling at other times is highly dependent on the presence of moonlight (see Fig.1 and Fig. 2)

6. On some nights there was no calling although the weather was fine and the moon visible for part of the night. These episodes are surprising and I have no explanation for them. For instance, the night of 29 Jan. 1986 was fine and cool, on the edge of the period of maximum calling in February, and the moon was visible from about 2200 hr, yet there was not a single call up to 15 min past midnight. On the other hand, it seems clear that rainy weather suppresses calling.

Discussion

The annual pattern of calling is clearly related to the breeding season. Belcher and Smooker (1936) state that "the peak of the breeding time falls between February and April but G.D.S. has found fresh eggs as late as July". My records of eggs on 19.IV.1976, 19.VI.1978, 10.IV.1987 and 22.III.1992 agree well with this. From July or August little parties of birds may be seen on the roads. One or two of the birds may seem smaller and with shorter tails than usual. I believe that these are young birds accompanying their parents on to the roads. At this time the numbers of birds on the roads increase (Quesnel 1990) and by October start to fall off again, presumably as the young birds die or disperse. I have no records of seemingly young birds after January, so by this time dispersal must be complete or the juveniles have become indistinguishable from their parents. Presumably, moult occurs during the period July - September, though I have no record of it.

In the eight years of observation calling has always ceased in late May or early June (Table 1). During the ensuing two months none of the various calls was heard. On the resumption of calling, the *wup-per-rah* call was the first to be heard with the *to-wee-oo* call following several weeks later. Thereafter the rate of calling built up slowly at first and then with increasing speed to the peak in February or March (Tables II and III). In Costa Rica the pattern seems to be much the same (Skutch 1972).

I first heard the drumming call on 3 March 1985 and thereafter heard it and saw the birds perform their ritual display several times in the breeding season of 1985 and again five times between 5 February 1986 and 12 April 1986. The display seems to be courtship for it is performed by both male and female when they are close together. By this time the *to-wee-oo* calls have increased in frequency over the low levels of September and October. Thus, the increase in calling coincides with the onset of courtship, and, presumably, territory selection as well. When the time for laying arrives early in the year calling is at or near its peak, and continues strongly thereafter until the rainy season arrives in June when calling ceases completely.

According to Skutch (1972) both sexes incubate during the day with the female alone incubating at night. This means that during incubation the male is free to patrol the territory and call from his accustomed stations. However, both sexes brood the young, though Skutch does not specifically say that both brood at night. When the male broods he is not free to patrol the territory, but I believe that the female then does this instead. It is very difficult to observe these birds in the dim light in which they perform most of their activities, but my observations show that the female too makes the *to-wee-oo* call, though it is more like *twee-oo*, fainter and higher-pitched than the male's call, and resembles the male's call at the end of a long series when they become fainter and often contracted to *twee-oo*.

However, the *to-wee-oo* call may have other functions. The conclusions that can be drawn from my notes are as follows:

1. The male's *to-wee-oo* call attracts females (only his mate?). 2. The *to-wee-oo* call is sometimes made in close proximity to the female while she is "drumming". 3. The *to-wee-oo* call can be made while the male is displaying to the famale. 4. The *to-wee-oo* call can occur in a sequence mixed with other calls. 5. The famale can answer the male's *to-wee-oo* call by calling *to-wee-oo* herself or with a *wut* or by "drumming", which can go on continuously while the male is calling.

Thus it appears that the male's *too-wee-oo* call is not simply a call to claim territory, but also attracts females and is part of courtship. Hence the intimate relationship between the annual pattern of calling activity and the breeding cycle.

The lunar pattern is, of course, determined by the lunar cycle. Simply put, the more moonlight there is, the more calling there is. The pattern seems clear and incontrovertible but the mere existence of biological rhythms that are influenced by the moon is controversial. Lieber (1979), in his book The Lunar Effect, gives the results of his own investigations and summarises many others, concluding that there is a lunar effect on many biological processes, including human behaviour. His studies of homicide, which he claimed clearly showed the influence of the moon, were criticised by Abell (1979) who did a statistical test on them and found them not significant. He also criticised Lieber's hypothesis about a biological tide and, it is true, Lieber gives little detail concerning the mechanism by which the supposed tide produces its effect. However, the influence of moonlight on the calling activity of the pauraque is not like the influence dealt with by Lieber. His graphs show, where they show any clear pattern at all, two or more peaks in the lunar month. Fig. 1 above shows just one peak and is therefore quite different. Other nightjars too are influenced by moonlight (Brigham and Barclay 1992).

My notes contain numerous references to the weather. For example, in December 1985 on 12th, 14th, 15th and 16th the pauraques called for at least some minutes in the period 1800 - 1930 hours with the moon in Day 1 to Day 5 of the cycle. On 18th, 22nd, 27th and 30th during Day 7 to Day 16 of the cycle when calling should have increased, there were no calls at all. On 18th and 27th the sky was altenately clear and cloudy; on 22nd and 30th the sky was overcast and drizzly. On 26th February 1985 on Day 8 of the lunar cycle when frequent calling would be expected, there was one call at 2115 hr and silence before and after. The weather was rainy. On 26th February 1986 on Day 19 of the cycle calling was in progress when I arrived home at 2230 hr; it went on continuously until 30 minutes after midnight at which time rain fell and the calling stopped abruptly. All these observations, and similar ones, suggest that rainy weather suppresses calling. On the other hand, on 29th and 30th January 1986 on Day 20 and Day 21 of the cycle there was not a single call all night from 1800 hr to midnight though both nights were clear and cool. Although the moon would not have risen until after 2100 hours and 2200 hours respectively, the lack of calling on these nights is strange, and suggests that not all the factors that influence calling have been recognised.

One final point seems worth mentioning. It is that the occurrence of calling just after sunset and just before dawn indicates the importance of light, not specifically moonlight, in stimulating calling. Also, the white wing bars and tail stripes of the male and the behaviour that displays them to the female would hardly have evolved if the birds were most active in near total darkness. It would seem therefore, that the pauraque is a bird superbly adapted to crepuscular conditions.

Acknowledgement

I thank Richard ffrench for reading an earlier version of this paper and suggesting a number of useful alterations for making it more effective.

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Book Reviews

A guide to the Birds of Trinidad & Tobago 2nd edition

Richard ffrench. Plates and drawings by John P. O'Neill, portraits by Don R. Eckelberry. 1991.
Comstock Publishing Associates, a division of Cornell University Press, Ithaca, New York. xvii + 426 pp.

I

This publication completely updates the first edition of this unique and indispensable work, which was published in 1973 and last revised in the early 1980's. Although that edition is still useable, the new edition contains many improvements and a plethora of new information.

Illustrations are the heart of a field guide. The original paintings were very good, but I feel that an opportunity has been lost to eliminate confusion due to crowding. All of the colour plates have been reprinted intact at the same size as in the first edition, even though the new edition features a larger page size. A better use of the larger page size would have been to reposition male-female pairs and to provide more space among species, especially on the plates of the hummingbirds, manakins, and tanagers. Many plates now depict rather small images of birds tightly clumped on pages with wide, unused margins.

John O'Neill painted one new colour plate for this edition, illustrating such gorgeous but unrelated species as Channel-billed Toucan and Scarlet Ibis. The exceptional whiteness of the paper on which the plates are printed adds to the brilliance of the colours.

All of the portraits from the first edition have been consolidated at the center of the book, following the plates, which makes finding them much easier than before. The portraits would have been even more accessible had they been inserted in phylogenetic order among the plates rather than being lumped after them. The present arrangement, however, still is better than that in the first edition. As in the first edition, 24 species are illustrated as line drawings. A dozen of these drawings have been recast in far better detail than in the first edition.

As expected in a new edition, the information presentd here has been updated and expanded from that in the first edition. The original introduction was so thorough that little could be added here except for a few timely updates, such as the recovery of certain species in Tobago. Several tables have been revised to reflect new information on the occurrence of migratory species in Trinidad and Tobago.

The body of the book consists of detailed accounts of more than 400 species of birds. Suffice it to say that ffrench has done another masterful job of pulling together the old and the new and has added descriptions of several species new to Trinidad and Tobago. Birders familiar with the first edition will appreciate the large amount of new information that ffrench has added to the existing species descriptions, drawing upon firsthand reports from competent birders as well as the literature base. When one considers the length of time required to produce a book of this nature, it is amazing to find that it includes records as current as February 1991, only six months before publication.

Among the other improvements, ffrench has incorporated the latest American Ornithologists Union names, substituting Whistling-Duck for Tree-duck, Common Piping-Guan for Trinidad Piping-Guan, Olivaceous Cormorant for Neotropic Cormorant, etc. Such consistency should ease the synonym problem for users comparing species descriptions among field guides. The titles of some of the plates have been change to more accurately reflect their content, e.g., "Large Raptors" instead of "Hawkes and Vulture", "Medium-sized and