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## Vocal Behavior, Morphology, and Hybridization of Australian Spotted and Yellow-rumped Pardalotes (Aves, *Pardalotus*)

LESTER L. SHORT,<sup>1</sup> JENNIFER F. M. HORNE,<sup>2</sup> AND  
RICHARD SCHODDE<sup>3</sup>

### ABSTRACT

In the course of varied Australian field studies during 1979 and 1980 we were able to devote some effort to investigating the vocalizations and other behavior of the closely related, largely allopatric Spotted Pardalote (*Pardalotus punctatus*) in Queensland, New South Wales, and Victoria; and to a lesser extent the Yellow-rumped Pardalote (*P. xanthopygus*) in Victoria. A few specimens were collected of birds whose voices were recorded on tape. Morphological studies of these and other specimens demonstrate the similarity of the two taxa. Their vocal repertory includes seven major vocalizations. Of these, six are calls, five in *punctatus* and three in *xanthopygus*. Probably all six calls are found in both forms. Differences in those of the calls found in both are nil or slight. Males of both species sing songs and abbreviated songs similar generally in quality and tone, but differing

between the two taxa in details of structure, pitch, and temporal arrangement of elements. Some vocalizations intermediate in form, pitch and timing, together with morphological data, indicate convergence of their characters in areas of contact in Victoria. Three of four specimens collected in Victoria are hybrids or likely hybrids as determined by their morphology and vocalizations. The vocal repertory as presented for the two taxa may be complete, but more data are needed, especially from *P. xanthopygus*. The extent of their hybridization, and hence their taxonomic status remain to be established fully, since they meet in three different regions (southwestern Australia, South Australia, and southeastern Australia), and the only detailed studies, reported here, cover but one region, and that only partly.

### INTRODUCTION

During the course of investigating hybridization in various Australian birds we attempted to gather some data on the behav-

ior of the closely similar Spotted Pardalote (*Pardalotus punctatus*) and Yellow-rumped Pardalote (*P. xanthopygus*). Our field studies

<sup>1</sup> Chairman and Curator, Department of Ornithology, American Museum of Natural History; Adjunct Professor, City University of New York.

<sup>2</sup> Research Associate, National Museums of Kenya, Nairobi, Kenya.

<sup>3</sup> Research Scientist, CSIRO Division of Wildlife Research, A.C.T., Australia.

took place sporadically, as we could take time from our major projects, in Queensland, New South Wales, and Victoria during August 1979 to January 1980. Previous studies of the behavior of these pardalotes have been sparse and lacking in many details (Chandler, 1961; Brunt, 1962; Richards, 1972) and further investigations are still needed. We present our data on their vocalizations and morphology in the hope that they will provide an appropriate framework for new investigations of these two morphologically similar pardalotes, which geographically replace each other generally but meet in southwestern Australia, South Australia, and southeastern Australia (see map in Salomonsen, 1961, p. 11). Pardalotes (genus *Pardalotus*) form a small passerine group with no close relatives, and the relationships of which are controversial (Morony, Bock, and Farrand, 1975; Schodde, 1975; Sibley, *in litt.*).

Horne made tape-recordings using a Stelavox Sp-7 recorder, a Schoeps CMC-45 condenser microphone, and a 76-cm. parabolic reflector. Audiospectrographic analysis was conducted with a Kay Elemetrics Sonagraph 6061-B. Playback was by means of a Sony cassette recorder using copies of our Stella-vox-recorded material. Dr. R. J. Swaby made available to us for audiospectrographic analysis a cassette copy tape of various of his recordings of *Pardalotus xanthopygus* and *P. punctatus*, obtained by use of diverse tape-recorders and microphones. The use of copy-tape material inevitably affects the analytical results, by reducing clarity and overtones, for example. However, the timing of the elements and aspects of their form and pitch are evident in those we have figured. We made specimen comparisons at the American Museum of Natural History.

We are especially indebted to Dr. Swaby for letting us use his recordings for analyses, and to Mr. Norman Robinson for his suggestions and aid. Mr. Richard Weatherly participated in the fieldwork in Victoria. Various other individuals too numerous to mention individually assisted us in the field, and Mr. Robert Stolberg aided us in our laboratories. We are grateful to wildlife authorities in Victoria for permission to obtain specimens. Short did his studies in Australia while he was a Visiting Fellow in the Australian

National University's Research School of Biological Sciences; funding for his fieldwork came from the Australian National University and the Leonard C. Sanford Fund of the American Museum of Natural History.

Throughout the text kHz is used to indicate kilohertz, AMNH, the American Museum of Natural History, and mm., millimeters.

## RESULTS

### VOCAL REPERTORY OF *PARDALOTUS PUNCTATUS* AND *PARDALOTUS XANTHOPYGUS*

We describe the vocalizations that we recorded from *Pardalotus punctatus*, *P. xanthopygus*, and possible hybrids between them, including for comparison some of *P. xanthopygus* (from South Australia, western Victoria, and New South Wales) kindly provided by Swaby. The repertory is not considered complete, although that of major vocalizations of *P. punctatus* may be so. Our discussion is in the framework of meaning, function, and motivation used in studies of Winkler and Short (1978). The arrangement is from structurally simpler, single-note calls to more complex calls and songs. Some comparisons are made with the Striated Pardalote complex (*Pardalotus striatus*, Short et al., *in prep.*), congeners that are broadly sympatric with both *P. punctatus* and *P. xanthopygus* (note the lack of such comparisons of *songs*, which are quite different in these two major pardalote groups).

**BEGGING CALL:** We include this call for the sake of completeness, although our only examples come from three young calling constantly while being fed by an apparent Yellow-rumped Pardalote in Bat Ridge Nature Reserve, 14 km. west of Portland, Victoria, on November 22, 1979. The only pardalote songs heard there were "weee-eee" songs typical of the Yellow-rumped Pardalote (see below). Begging calls tend to be conservative, that is, very similar or identical in closely related species of diverse taxonomic groups (e.g., woodpeckers, see Winkler and Short, 1978). Hence the Spotted Pardalote Begging Calls are apt to prove similar or identical with those we describe. The call (fig. 1A) is variable in the emphasized pitch and composed of short, fast notes 0.02 to 0.025 second in

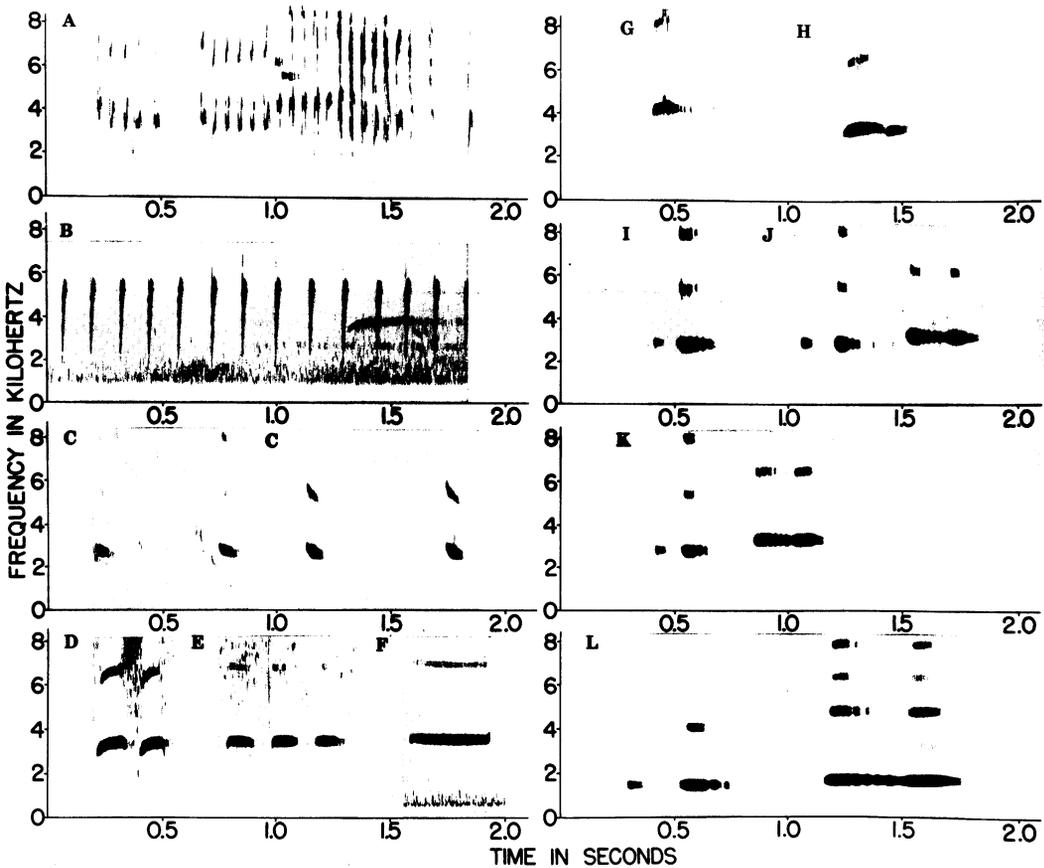


FIG. 1. Wide-band sonagrams of calls and songs of Australian *Pardalotus punctatus* and *P. xanthopygus*. A. Begging Call, young of *xanthopygus*, Bat's Ridge, Victoria, November 22, 1979. B. Fast Chip Call, male *punctatus*, Orphan Gully, Queensland, September 21, 1979. C. Short Weep Call, notes of *punctatus*, Orphan Gully, Queensland, September 21, 1979, then two of hybrid male *xanthopygus* × *punctatus*, Mitre, Victoria, November 6, 1979. D. Long Weep Call, double note of male *punctatus*, near Heywood, Victoria, November 24, 1979. E. Long Weep Call, triple note, of hybrid male *xanthopygus* × *punctatus*, Mitre, Victoria, November 6, 1979. F. Whee Call, male *punctatus*, Orphan Gully, Queensland, September 21, 1979. G. Weet Call, near Heywood, Victoria, November 24, 1979, probable *punctatus* (possibly same bird as fig. 2H). H. Weet Call, longer form, *punctatus*, Terang, Victoria, November 28, 1979. I. Sa-weet Abbreviated Song, male *punctatus*, Terang, Victoria, November 28, 1979. J. Sa-weet Ba-bee Song, male *punctatus*, Orphan Gully, Queensland, September 21, 1979. K. Sa-weet Ba-bee Song, male *punctatus*, near Heathmere, Victoria, November 25, 1979. L. Same song as K, but read twice the stated frequency and twice the stated time (sonagram at 0–16 kHz, rather than 0–8 kHz).

duration. Essentially each note contains fast-rising, partially falling, then rising, peaking and dropping elements. Emphasis is on the partial drop and following rise to a peak at 3.8 to 5 kHz. Some notes are simply rapid, peaked, and inverted V-shaped; others are noisy and fast with structure obscured sonographically. Harmonic tones are evident, as in most begging calls, yielding its high piping

quality. These variations likely reflect proximity of the feeding adult and relative hunger of the young. Notes are uttered at 15 to 17 per second and may be continuous or in bursts. Localization of the calling young and the eliciting of feeding by the adults are obvious functions of the call.

**FAST CHIP CALL:** Our only examples of this call are from a male Spotted Pardalote

strongly stimulated by song playback at its nest near the North Branch of Dalrymple Creek, 26 km. north-northeast of Warwick, southern Queensland on September 21, 1979. As he perched, hopped, and stamped his feet at the entrance to the nest he displayed toward the "singing intruder" represented by the recordist, erecting the red rump and spotted crown feathers (similar in part to the display described by Richards, 1972, p. 155), and chip-calling in bursts and in long series of up to one minute continuously, or with but short pauses over a 10-minute period. He approached the recordist several times, right to her feet, turning about, calling and displaying. The notes (fig. 1B) are sharp, mechanical chips but 0.01 to 0.02 second in duration, at a tempo of 8 to 9 per second. The note sonographically resembles an exclamation point without the basal dot, but structurally is a very fast, soft drop from 7 or even 8 kHz to about 1.9 kHz, followed instantly by a rise to the loud peak, continuing to the end of the note at 5.1 to 5.5 kHz. Most sound is in the rise and peak, and in fact the initial drop is lacking in some (less well recorded) recordings. Richards (1972, p. 155) noted "zit" or "tik" calls from displaying Spotted Pardalotes, that may represent the Fast Chip Call just described. Preceding the male's Fast Chip Call he uttered several Whee Calls (see below). He also sang intermittently. The female came and went during the male's display, several times adding her Short Weep Calls to his utterances. We cannot determine the functions and meaning of the Fast Chip Call on the basis of this one observation, but it clearly is associated with visual displays of the male at the nest. Fast Chip Call notes are unlike any notes of the Striated Pardalotes that we studied much more intensively.

**SHORT WEEP CALL:** Notes given in diverse situations and rendered "weep" are often of very low volume. Usually uttered by Spotted Pardalotes in series (fig. 1C) of two to 35 or more, they consist of relatively short, usually down-dropping sound at 2.75 to 3.8 kHz, with a weak to moderate overtone at 7 kHz or more. Each is 0.035 to 0.085 second (mean of 32, 0.055 second) in duration. In series the tempo varies, but approximates 2 per second with an interval of 0.37 to 0.66 second between notes. We have recorded the same

call (fig. 1C) from a backcross hybrid male Yellow-rumped Pardalote (see below) west of Mitre, Victoria, on November 6, 1979, hence it likely occurs in both taxa. These soft notes often mark interactions of a pair, especially near the nest, and apparently are the "Pe he" notes of Richards (1972, p. 155). A female may give Short Weep Calls as the male sings nearby. Thus, pair contact may be a function of this call. It also may be uttered by the male interspersed among his songs without the immediate presence of the female, perhaps in an attempt to establish contact with her.

**LONG WEEP CALL:** This vocalization resembles the Short Weep Call, often being of low volume, but it is longer, it usually rises rather than falls in pitch, and it frequently is uttered rapidly in a two-note or three-note series. The few recorded examples preceded songs and could have been uttered by either the singing male or a nearby mate, or an interactive second male. Five examples of Spotted Pardalotes show (fig. 1D) rising pitch in each of two notes, the notes being 0.05 to 0.13 second in duration, giving 0.20 to 0.30 second for their total duration. The frequency rises from 3.1 or 3.2 kHz to 3.25 or 3.35 kHz. Four samples, all from the backcross hybrid male Yellow-rumped Pardalote west of Mitre, Victoria, on November 6, 1979, contain one to three notes (fig. 1E) at a pitch of 3.35 to 3.5 kHz, slightly higher than those of the Spotted, and differing by their even, rather than rising pitch. The notes are 0.10 to 0.125 second in duration, and the three-note series are rendered in 0.48 and 0.51 second. Five double notes of Long Weep Calls obtained by Swaby at Bunn's Bore near Bordertown, South Australia, on May 19, 1974, appear similar to those described from the Mitre, Victoria, Yellow-rumped Pardalote; songs recorded by Swaby that day at Bunn's Bore are of the high-pitched "wee-eee" type (see below) ascribed to the Yellow-rumped Pardalote. These Long Weep Calls from Bunn's Bore are 0.07 to 0.13 second in duration, the second note of each pair being shorter than the first. Their pitch is at 3.3 to 3.4 kHz, near that of those described for the Spotted Pardalote, but there is no rise in pitch. Until there are more data it seems prudent to draw no conclusions from the apparent differences just noted. The function of this call in regard

to the Short Weep Call particularly needs study.

**WHEE CALL:** A single, double, or occasionally a series call, a whistled "wheee," was associated with periods of excitement such as human intrusion near the nest, and playback of songs at a male. The 10 notes studied (fig. 1F), all of *punctatus*, are 0.245 to 0.36 second at an even pitch or dropping slightly between 3.55 and 3.7 kHz initially and 3.45 and 3.55 kHz terminally, and show a weak harmonic tone at 6.75 to 6.9 kHz, or more usually, none. In series they are uttered at a variable tempo with intervals of 0.12 to 1.27 second. The pitch is higher than that of the full song (see below), and its even pitch lacking modulation renders it unlike any other calls of the Spotted, Yellow-rumped or Striated pardalotes. This call preceded several of the Fast Chip Calls of the male displaying at the Dalrymple Creek site mentioned under those calls.

**WEET CALL:** This loud note is associated closely with either abbreviated (eight cases, "sa-weet," see below) or full (nine cases, "sa-weet ba-bee," see below) songs of Spotted Pardalotes. It is the first of the songlike calls to be considered. A "weeet" or "weee-eet" describes the call (fig. 1G) which often has a terminal ("-eet") element (fig. 1H). The duration of the call is 0.09 to 0.20 second, or, with the "eet," 0.25 to 0.29 second. Its frequency is between 4.25 and 4.65 kHz, mainly 4.3 to 4.5 kHz, with overtones above 8 kHz (weak to strong), at 12.5 to 13.5 kHz (stronger), and sometimes at 16 kHz. In form the note shows a distinctive, more or less pronounced, rise initially then an almost imperceptible fall; the terminal "-eet," when present (fig. 1H), begins below the tail of the longer initial "weee" and rises slightly before ending. Consecutive calls have not been recorded, rather the Weet Call precedes or follows other forms of song by 1.0 to 1.8 second. No Weet Calls have been found in the material of *xanthopygus* available to us. A single Weet Call note comprises the initial element in some variant full songs described below. We have been unable to find behavioral differences associated with variation in the song form of Spotted Pardalotes; some individuals in a locality may sing only typical songs, while others may switch back and forth among two or even three types of

song. Individuals stimulated by playback often show greater variation in their songs than prior to playback.

**SA-WEET ABBREVIATED SONG:** The Sa-weet is a double-noted introduction to the full song of *Pardalotus punctatus* that may be uttered by itself, usually interspersed among full songs or full songs and Weet Calls (the Weet Call also could be considered an Abbreviated Song, or rather a replacement Abbreviated Song, as it is not part of the typical song). The 29 examples of Sa-weet Abbreviated Songs (fig. 1I) studied sonographically, when compared with 43 examples of Sa-weets from full songs show that these Sa-weets are equivalent except that the Abbreviated version varies a bit more overall, and tends to be longer, note for note, than when preceding the "Ba-bee" of the full song. The 29 Sa-weet Abbreviated Songs are 0.22 to 0.265 second in duration, with the "sa" taking 0.015 to 0.07 second and the "weet," 0.105 to 0.16 second. The "sa" is at 2.75 to 2.85 kHz, and the "weet" at 2.65 to 2.8 kHz. Overtones usually are absent or at most weak on the "sa" at 5.5 and 7.8 kHz, and weak to moderate at 5.2 to 5.3 and moderate to strong at 7.6 to 7.8 kHz on the "weet." The shorter "sa" often is weaker than the "weet," and may be inaudible in distantly recorded calls; it tends to rise slightly in pitch. The "weeet" is strong and either level or wavering somewhat in pitch with occasional signs of modulation. There always is a gap between the two elements exceeding 0.05 second in duration.

**SA-WEET BA-BEE SONG:** This is the typical song (fig. 1J, K) of the Spotted Pardalote. Brunt (1962) was correct in declaring that only one bird, not two (see Chandler, 1961) utters the full Song, and in our experience it is always given by the male. At a distance the weakest element, the "sa," tends to drop out; the "ba-bee" often runs together such that a drawn out single note is heard, but overtones always reflect the dual nature of that portion of the song. Overall the full song is but 0.67 to 0.80 second (mean 0.747 second) long in 43 examples from Queensland to Victoria, and it shows relatively little variation (compare fig. 1J and 1K). The Sa-weet Abbreviated Song has been analyzed above, and the "sa-weet" of the full song is similar but

shorter, the "sa" lasting from 0.01 to 0.06 second and "weet," from 0.065 to 0.12 second in duration. The break or gap between the "sa" and "weet" is 0.05 to 0.12 second, with a mean of 0.09 second. The Sa-weet is followed in 0.17 to 0.24 second (mean 0.209 second) by the loud, pulsed, modulated Ba-bee ("baa-a-bee-ee-ee," or "baa-a-ee-eee-ee") of 0.24 to 0.33 second (mean 0.29 second) duration. The Ba-bee may be connected throughout by sound, but usually the "Ba" ends in several pulses of sound at 0.07 to 0.19 second, after which there may be a slight break before the "bee."

The frequency of the "sa" is at 2.75 to 2.9 kHz (mean 2.83 kHz), the "weet" at 2.6 to 2.85 kHz (mean 2.72 kHz), the "ba" at 3.1 to 3.3 kHz (mean 3.19 kHz), and the "bee" at 3.0 to 3.3 kHz (mean 3.17 kHz). The first two notes thus are at a distinctly lower pitch, usually with a slight drop from the "sa" to the "weet." The weaker "sa" lacks harmonic tones (in 31 of 43 cases), or they are weak, whereas the "weet" shows overtones at 5.15 to 5.4 kHz (mean 5.25 kHz), usually a stronger one at 7.5 to 7.85 kHz (mean 7.75 kHz), and often others at about 10.4, 13.4, and 15.1 kHz. The "ba" and "bee" essentially are at one pitch (equal in 18 cases, the "ba" is barely higher in 13, a trifle slower in 2 of 33 checked for this feature). Overtones are usually weak to strong but they delimit the "ba" and "bee" more clearly than does the fundamental tone. It can be seen clearly from figure 1L, which provides analysis up to 16 rather than 8 kHz, that the alternate overtones are emphasized (at about 9 and 15 kHz) and contribute substantially to the sound characterizing this song.

The functions of the song undoubtedly are complex, as in the alternating of this form of the song with the previous two forms. Reaction to playback of song is intense and often long-lasting (a relatively infrequently singing male, upon playback, may sing much more frequently not only that day, but the next as well, with no further playback attempted), inferring a territorial function, and, with correlated visual displays, a definite aggressive motivation (Winkler and Short, 1978). The singing male usually actively seeks the source of the playback, approaching and circling the recordist at a range of 1 meter or even less. The female may or may not be attracted to

the vicinity of the male, whether singing without playback or in response to playback. However, the loud, penetrating song and its constant repetition provide a clear indication of the singer's location to its mate, and location and perhaps stimulation of the female, pair-bond maintenance and other functions may be served by this song.

**WIT WEE-EEE SONG:** This is the Yellow-rumped Pardalote's equivalent (fig. 2A) of the Spotted Pardalote's Sa-weet Ba-bee Song. When uttered in full it is a much longer, if structurally simpler song than that of *punctatus*, with a duration of 1.12 to 2.28 seconds (mean 1.63 seconds). In 30 full songs the short, weak "wit" (it may be lacking, see below) is 0.02 to 0.07 second (mean 0.054 second) in duration, and the "wee-eee" is 0.21 to 0.32 second (mean 0.276 second), the "wee" lasting 0.10 to 0.21 second and the "eee" 0.01 to 0.115 second. Some temporal variation is due to the weakness of the "wit" and "eee" elements, only part of which may be loud enough to reproduce well sonographically. There also is considerable variation in the length of the song (fig. 2A, B) due to the variable interval between the "wit" and the "wee," that being 0.82 to 1.92 second (average 1.31 second). Thus the two main parts of the song are separated by at least several times the interval between the two main parts ("sa-weet" and "ba-bee") of the Spotted Pardalote's song.

In pitch the initial "wit" is variable, between 2.4 and 3.1 kHz, but averaging 2.91 kHz, about at the maximum for the "sa" note of the Sa-weet Ba-bee Song. The "wee-eee" rather consistently shows a drop in pitch (in 27 of 30 songs), averaging 3.74 kHz for the "wee" and 3.58 kHz for the "eee" elements; the low extreme of both "wee" and "eee" barely reaches the upper frequency limit of the "ba-bee" in the Spotted Pardalote's song, the range being 3.15 to 3.9 kHz for the "wee" and 3.0 to 3.8 kHz for the "eee." Harmonic tones are lacking in sonagrams from copies of Swaby's recordings, but they are clearly marked and strong (at 5.8 and over 8 kHz for the "wit," and, especially, at 7.5 to 7.25 kHz for the "wee-eee") in the hybrid Mitre, Victoria, male discussed below.

The "Wit" note is sometimes uttered apart from the full song (examples by Swaby from

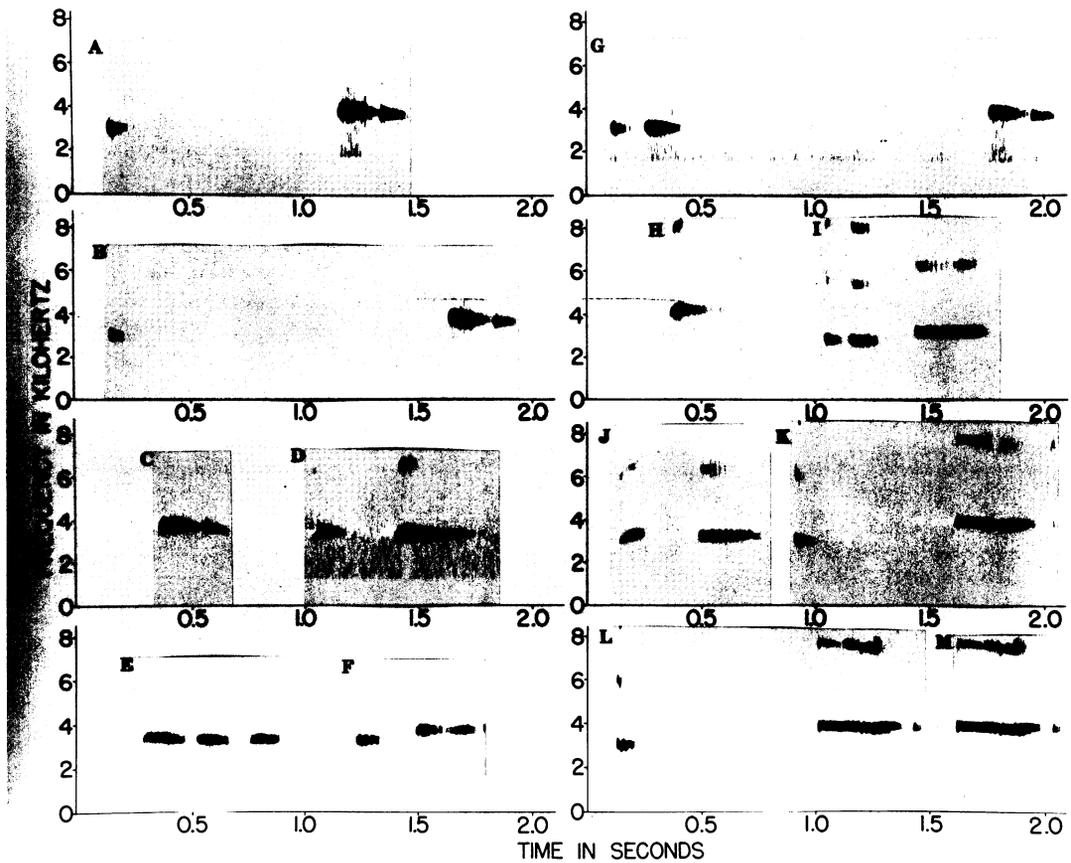


FIG. 2. Wide-band sonograms of more calls and songs of Australian *Pardalotus punctatus* and *P. xanthopygus*. A. Wit Wee-eee Song, *xanthopygus*, Sedan, South Australia, August 31, 1975 (Swaby). B. Longer Wit Wee-eee Song, *xanthopygus*, Swan Reach, South Australia, May 1977 (Swaby). C. Wee-eee Song, *xanthopygus*, Tailem Bend, South Australia, June 1, 1975 (Swaby). D. Variant song ("eep-beeee"), male *punctatus*, Orphan Gully, Queensland, September 21, 1979. E. Variant song ("wee-eee-eee"), *xanthopygus*, Kangaroo Island, South Australia, March 31, 1974 (Swaby). F. Possibly hybrid *punctatus* × *xanthopygus* song, Nelson, Victoria, September 12, 1967 (Swaby). G. Possibly hybrid *punctatus* × *xanthopygus* song, Overland Corner, South Australia, October 8, 1973 (Swaby). H. Weet Call, likely hybrid male *punctatus* × *xanthopygus*, Heywood, Victoria, November 24, 1979. I. Sa-weet Beee Song, likely hybrid male *punctatus* × *xanthopygus*, Inglewood, Victoria, November 5, 1979. J. Weet-beee Song variant, same male as I. K. Wit Wee-eee Song, male hybrid *xanthopygus* × *punctatus*, Mitre, Victoria, November 6, 1979. L. Another song, same type as K, of same male. M. Wee-eee Song, same hybrid male as in K.

Hattah Lakes, Victoria, August 30, 1978), although not to the same extent as in the Sa-weet of the Sa-weet Ba-bee Song. In contrast the Wee-eee is uttered, apparently frequently, without the Wit; the lack of a Wit note may be ascribed to lack of focus of the microphone or distance from the bird, as this note is relatively weak, but our Mitre recordings were at close range and we could hear songs uttered

lacking the Wit introductory note. This is in contrast to the Ba-bee of the Sa-weet Ba-bee Song, which appears not to be given apart from the Sa-weet elements.

It should be noted that certain Wee-eee Songs (lacking the "wit," see fig. 2C) closely resemble the "weet-it" version (nearly double-noted version) of the Spotted Pardalote's Weet Call. The two are of the same duration

and general form, the Wee-eee differing from the "wee-it" only in its slightly higher pitch and distinct downward rather than upward inflection at the end.

**VARIANT SPOTTED PARDALOTE SONGS:** Several songs do not match the descriptions just provided in all of their characteristics. A male from Orphan Gully, Queensland, just prior to giving the typical song shown in figure 1J, uttered an "eep-beee" (fig. 2D). This latter vocalization is loud and somewhat resembles the full Sa-weet Ba-bee Song in overall form, but it lacks the "sa" note, the "eep" is not like the second "wee" note of the full song, and the drawn out "beee" is continuous, with no indication of a break. The initial "eep" rises peculiarly (somewhat like a Weet Call, but that call is longer and usually higher pitched), and its frequency (3.35 kHz) is well above that of the "Sa-weet" introductory notes of the full song. The "beee" is, at 0.32 second, within the range of the full "Ba-bee" of a typical full song, and it is at the high extreme of pitch (3.3 kHz) of the "Ba-bee." There are several pulses indicated, as in the full song. One significant aspect of this variant song is the slightly dropping pitch from the first to the second note, which, with the high pitch of the first note imparts a bit of the quality of a Yellow-rumped Pardalote's song. Another point is its occurrence in the same individual singing typical *punctatus* full songs, showing that *punctatus* is capable of giving songs tending toward those of *xanthopygus* in at least some aspects.

We note that songs recorded September 3, 1973, near Karoonda, South Australia, by Swaby are at the extreme high pitch of those of *P. punctatus* from elsewhere, although the five examples studied are in other respects typical of Sa-weet Ba-bee Songs. They are rather weak, without overtones, in our copy tape, hence we do not show the sonagrams, but the pitch of the "sa" was at 2.8, 2.85, 2.85, 2.9, and 2.95 kHz in the five songs, the "wee" is at 2.85 in one and 2.9 kHz in four examples, the "ba" is at (3.3 kHz), or just above (3.35 kHz) the extreme high of 3.3 kHz for *punctatus*, and the "bee" is within the range of *punctatus*. This variation may prove to be within that for *punctatus* in South Australia, but geographical proximity there

between *punctatus* and *xanthopygus* makes any convergence (i.e., the higher pitch tending toward that of *xanthopygus*) noteworthy.

**VARIANT YELLOW-RUMPED PARDALOTE SONG:** Among the vocalizations on a tape provided by Swaby is a three-noted, loud song, a "wee-eee-eee" (fig. 2E), uttered March 31, 1974, on Kangaroo Island, South Australia, by a presumed Yellow-rumped Pardalote. This song, 0.59 second in duration, contains notes consecutively 0.18, 0.14, and 0.12 second in duration, and separated by gaps of 0.05 and 0.10 second. The three notes show only a very slight drop in pitch, from 3.4 to 3.35, 3.35 to 3.3, and then 3.3 to 3.25 kHz. They could be considered an extended Wee-eee Song (lacking the introductory Wit note), but, although their pitch is in the lower range of that song, the notes are farther apart (the first two together are 0.37 second in duration, the maximum for the Wee-eee Songs at hand being 0.32 second), the second note is too long, and there is a third note. There is resemblance to a three-noted Long Weep Call of *punctatus* (fig. 1E), but the Wee-eee-eee notes lack the regular form and shape of those notes sonographically, and show a suggestion of the frequency modulation that marks the Ba-bee portion of the full song of *punctatus*, and to a lesser extent the Wee-eee portion of that of *xanthopygus*. We tentatively consider this vocalization a variant form of the song of the Yellow-rumped Pardalote; Spotted Pardalotes do not occur on Kangaroo Island.

**POSSIBLY HYBRID SONGS:** Two series of songs provided us by Swaby are of interest in that they exhibit peculiarities of structure suggesting intermediacy, or at any rate a tendency in songs presumed to be of one species, toward the song of the other species. One array consists of songs from Nelson, southwestern Victoria, recorded by Swaby on September 12, 1967. In form and sound the song (fig. 2F) appears to be a distantly recorded Sa-weet Ba-bee Song, i.e., of the Spotted Pardalote, but lacking the "sa" note. The proximity of the initial "wee" to the "ba-bee" (interval 0.17 second in all three examples) is that of the Sa-weet Ba-bee Song. The initial "wee" is at 3.25 to 3.35 kHz in the three examples, and this frequency is considerably above that of the Sa-wee in a typical *punc-*

*tatus* song. There is a rise in pitch from the Weet to the Ba-bee, which is virtually at an even pitch, at 3.65, 3.7 and 3.85 kHz, in these songs, the pitch being well above that of the Ba-bee of *punctatus* songs and within that of the Wit Wee-eee Song of *xanthopygus*. Thus, in effect, these songs are like that of *punctatus* but pitched like that of *xanthopygus*.

Among songs recorded by Swaby at Overland Corner on the Murray River in October 1973 are a group from October 8 that are typical in every way of those we have described for *P. xanthopygus*, namely drawn out Wit Wee-eee Songs. However, on both October 5, and 8, 1973, he tape-recorded the voice of a pardalote uttering a distinctive song (fig. 2G) with attributes of both the Sa-weet Ba-bee and Wit Wee-eee songs. This song may be rendered Sa-weet Wee-eee, and five examples show it to be variably long (1.7 to 2.13 seconds, in the range of *xanthopygus*) with an interval of 1.12 to 1.53 second between the "weet" and the "wee" (interval that of *xanthopygus*). The first, "sa" note is 0.02 to 0.08 second (overlaps time of both "sa" and "wit," to longer than either), and the "weet," coming 0.07 to 0.11 second after the "sa," is 0.125 to 0.16 second in duration (the "weet" exceeds the duration of both "wit" and "weet" notes, respectively of the song of *xanthopygus* and of *punctatus*). The Wee-eee, at 0.27 to 0.285 second, with the "wee" at 0.105 to 0.15 second and the "eee" at 0.075 to 0.1 second, is entirely within the range of *xanthopygus* in these parameters. In frequency all notes exceed that of *punctatus*, and fall within the range of *xanthopygus*, with the "sa" at 3.05 to 3.15 kHz, the "weet" at 3.1 to 3.2 kHz and descending slightly by up to 0.1 kHz, the "wee" at 3.8 to 3.9 kHz descending by 0.05 to 0.1 kHz, and the "eee" at 3.7 to 3.8 kHz and descending very slightly. Effectively the second "weet" note has been added to a song otherwise like that of *xanthopygus*; the overall effect is that of a long-interval, high-pitched *punctatus* song with *xanthopygus*-like elements. Certainly the "weet" element otherwise is lacking in the repertory of *xanthopygus* as currently known, and is equivalent in structure to the "weet" note of a *punctatus* Sa-weet Ba-bee Song.

We suggest that these peculiar songs may

be of hybrids, and that studies of the status of *P. xanthopygus* and *P. punctatus* in the vicinity of Nelson and Overland Corner would be productive.

#### VOCALIZATIONS OF THREE COLLECTED MALES

We recorded vocalizations of three males that we later collected, their behavior or morphology or ecology causing us to question their identity. Their vocalizations are described here, and their morphology discussed below.

Male, 5 km. south-southeast of Heywood, Victoria (AMNH 824921). Within but near the edge of second growth moist eucalypt woodland we found numbers of Spotted Pardalotes, as determined by song, on November 24, 1979. One of the males in this area attracted our attention by its pale rump that appeared neither yellow nor rusty. We sought this individual, tape-recording as we did so. A number of vocalizations were recorded, but are not definitely ascribable to the bird in question (e.g., the Weet Call, fig. 1G). We finally obtained a clear view of the bird and recorded it while in view up to the time it was secured. Its vocalizations include a Weet Call (fig. 2H), uttered before a Sa-weet Abbreviated Song; the Weet is a bit low in pitch (4.1 kHz) for typical *punctatus*, as even other calls from the same locality are pitched above 4.2 kHz. Not much can be made of this, for we have no Weet Calls of *xanthopygus*. We recorded eight Abbreviated Sa-weet Songs and three full songs from the male we sought. The Sa-weet Songs are typical of those described for *punctatus* in all respects, although the pitch, particularly of the weet element, is at the low end of the spectrum (some at 2.6 kHz) in the sample of *punctatus* Sa-weets available to us. The full songs are *punctatus*-like also, although they too tend to be low-pitched (two of three "sa" elements at 2.65 kHz). We conclude from the available vocal data for this male that its repertory was *punctatus*-like, ascribing no cause for the tendency of its vocalizations toward a low pitch. Other vocalizations from this site include two Long Weep Calls, three Weet Calls, two Sa-weet Abbreviated Songs, seven Sa-weet Ba-

bee Songs, and two odd songs, not well recorded, rendered "weep-bee." All are typical of *punctatus* except the last, odd songs. These are unusual in the even pitch, at 3.25 kHz, of the weaker, short (0.04 to 0.06 second) initial note and of the longer, pulsating "bee" note, which closely resembles the "ba" element of Sa-weet Ba-bee Songs. We regard these odd songs as variant *punctatus* songs (both unfortunately show too much background noise to be figured).

Male, 4 km. northwest of Inglewood (50 km. northwest of Bendigo), National Museum of Victoria collection. On November 5, 1979 this bird and its mate attracted our attention because of the habitat in which we saw them which was mallee scrub and partly second growth. The male called and sang vigorously, and since we saw no other individual than its mate, we attribute all the vocalizations we describe to the two birds. Both appeared *punctatus*-like in plumage. We recorded Short Weep Calls (probably of the female), eight Weet Calls, five Abbreviated Sa-weet Songs, eight full (Sa-weet Ba-bee) songs, and five variant Weet-bee Songs. The songs and Weet Calls were uttered by the male of the pair. The Weet Calls and Short Weep Calls differ not at all from those described above for *punctatus* (and for *xanthopygus* in the case of the latter call). The Sa-weet and Sa-weet Ba-bee songs also fall within the range of variation of *punctatus* (a Sa-weet Ba-bee Song is shown in fig. 2I), although the Ba-bee section of the full song is rather continuous, more a "beeeeee" with no or almost no break. The variant Weet-bee Songs (fig. 2J) resemble a variant *punctatus* song from Queensland (fig. 2D), and even more closely, the Weep-bee variant song described above for the Heywood male. The rising first note at 3.1 to 3.5 kHz, the slightly lower but very evenly pitched, continuous beee element, and temporal relations of the elements are noteworthy. We see no strong indication of wide spacing of the notes, increased pitch of the song, or a broken beee element, dropping in pitch, any of which might represent a tendency toward *xanthopygus*. Rather the Weet-bee Songs are considered as a variant *punctatus* song, pending further elucidation of the repertory of *xanthopygus*.

Male, 3 km. west of Mitre (41 km. west of Horsham), AMNH 824922. This male, apparently alone, sang and called in dry sclerophyll woodland dominated by *Eucalyptus leucoxylon* and *E. baxteri*. We analyzed a series of Short Weep Calls (fig. 1C), four Long Weep Calls of one to three notes (fig. 1E), four Wee-eee Songs (fig. 2M), and nine Wit Wee-eee Songs (fig. 2K, L). The Short Weep and Long Weep calls resemble those of *punctatus*, as discussed above, comparable calls of *xanthopygus* being unavailable for analysis. In form the songs clearly resemble those of *P. xanthopygus*, with a short preliminary note followed after a pause by a double note that drops. The pitch of all elements is that of *xanthopygus* (Wit, 2.85–3.05 kHz; Wee-eee, dropping 3.9 to 3.65 kHz). However, in their temporal facets and in some aspects of structure the songs are not quite like those of *xanthopygus*. The Wee-eee Songs and element of the full song are longer than in *xanthopygus* in six cases. The Wit note of the Wit Wee-eee Song in seven of nine cases (see fig. 2K) is separated from the Wee-eee by less than the 0.82 second minimum in *xanthopygus* songs (the interval is 0.66 to 0.94 second in the bird from Mitre, 0.82 to 1.92 second with a mean of 1.31 second in 30 *xanthopygus* songs). Well recorded songs of both types from the male from Mitre show a separate terminal element following the Wee-eee (fig. 2L, M), and, preceding this terminal element, an even-pitched element at a frequency above the dropping "eee" segment (fig. 2K, L, M). The Wee-eee portion also is well connected in most songs from the Mitre bird, giving a "weeeeee" sound rendering it difficult to discern a break. While all these variations are not in the direction of *punctatus* songs, the temporal shortening of the song is. That shortening and the observed temporal variation noted above in recordings by Swaby from Nelson and Overland Corner, lead us to suspect that there is *punctatus* influence shown in the songs of the male from Mitre.

#### MORPHOLOGY AND HYBRIDIZATION

*Pardalotus xanthopygus* is a trifle larger (longer winged, longer tailed) than is *P. punc-*

*tatus*; its bill is the same length but tends to be slightly less broad, and less deep. The two taxa differ in a number of features, but these are such that they well may be genetically closely tied. Basically, *xanthopygus* is paler and *punctatus* is washed with buffy cinnamon to chestnut; reduction of this single color array in *punctatus* would render it into "*xanthopygus*." Dorsally, the spotting is similar in the two, but the spots are washed yellowish buff to cinnamon in *punctatus*. The lowermost back and rump are yellow in *xanthopygus* and cinnamon to chestnut cinnamon in *punctatus* (but these areas may be underlain with yellow in *punctatus*, which has yellow undertail coverts). Both are yellow on the undertail coverts, but these are cinnamon- or buff-tinged in *punctatus*. The underparts of *punctatus* are variably washed in cinnamon buff or creamy buff, whereas *xanthopygus* has such color extremely reduced, mainly appearing whitish or buffy whitish below. Finally, the yellow throat of *xanthopygus* is less golden, that of *punctatus*, more golden yellow. All of these traits involve richness of (mainly cinnamon) color, and it may be that they are affected by very few genes or gene combinations.

The colors are affected by wear, chestnut cinnamon or buff cinnamon fading to buff throughout; the back spotting of very worn *punctatus* may show little buff, closely resembling the white-spotted condition of *xanthopygus*. Some worn *punctatus*, e.g., male AMNH 698754 from Selby, Victoria, approach *xanthopygus* not only in color of the back spots, but in yellowish appearing in the (pale cinnamon) rump and in the paleness of the underparts. These factors, taken with the very close resemblance of the two taxa in all other traits (some of them involving complex patterns and strong color markings), make the determination of hybrids difficult.

Measurements also disclose very little difference between these two pardalotes. Comparing 16 adult males of *P. punctatus* from New South Wales and Victoria taken September to January with 15 males of *P. xanthopygus* from Victoria obtained in September to November gave these mean results, *punctatus* preceding *xanthopygus* in each case: wing length (chord) 57.19 vs. 57.87 mm.; tail

length, 28.91 vs. 30.53 mm.; bill length (exposed culmen) 6.89 vs. 7.23 mm.; bill width across nostrils, 4.29 vs. 4.11 mm.; and bill depth at center of nostrils, 3.91 vs. 3.67 mm. Overlap in all cases is very extensive (even complete in bill length and bill depth). Even in the case of the character showing greatest difference, tail length, 10 of 16 *punctatus* fall within the range of *xanthopygus* and 10 of 15 of the latter fall within the range of *punctatus*. What we see then are tendencies, that is, for *xanthopygus* to attain slightly greater tail, wing and bill lengths, with *punctatus* having a slightly wider, deeper bill. The mensural differences, if indeed larger samples were to prove them valid, are trivial, not even approaching those found between subspecies of one species. These data clearly offer no help in determining hybridity of any individual bird.

Four male specimens were obtained in the course of our studies in Victoria during November 1979. They were compared with more than 50 males of each of *P. punctatus* and *P. xanthopygus* representing all seasons of the year. The morphology of the newly collected birds is treated in order of the date of their collection.

Male, 4 km. northwest of Inglewood (50 km. northwest of Bendigo), National Museum of Victoria collection. This bird was studied and its voice recorded November 5, 1979, in mallee scrub, where it was singing (see above), accompanied by a female, apparently its mate. It weighed 8.4 grams and its testes measured 2 by 1 mm. Its bill is longer than that of either form (from samples used in comparison); at 7.8 mm. the bill length might be taken as an indication of *xanthopygus* influence, but bill lengths overlap in our samples (though averaging 0.34 mm. longer in *xanthopygus*). The yellow of the throat has a golden tone and some cinnamon traces posteriorly. Ventrally it is pale buffy cinnamon, less richly colored than *punctatus* and within the range of *xanthopygus*. The undertail is richly colored, golden yellow with strong cinnamon edging at the base. Its rump is rich cinnamon rufous tending to chestnut, well within the range of *punctatus*. The back spotting shows but slight buffy edging, espe-

cially posteriorly and in the scapular areas. Thus, possible *xanthopygus* influence is evident only in ventral and dorsal color, and in bill length. The specimen does not appear exceptionally worn (which would result in fading and an "approach" to *xanthopygus*), and we consider this bird a likely hybrid of *punctatus* × *xanthopygus* or a backcross product of such a hybrid crossed with *punctatus*.

Male, 3 km. west of Mitre (41 km. west of Horsham), AMNH 824922. Observed, voice recorded, apparently alone in open dry sclerophyll woodland on November 6, 1979. It weighed 8.6 grams and its testes (damaged) measured maximally 5 mm. In measurements this specimen falls within the range of overlap between *punctatus* and *xanthopygus*, except for tail length (31.3 mm.), in which it slightly exceeds the maximum measurement for *punctatus*. In its coloration this specimen falls completely within the range of variation of *xanthopygus* except for its undertail coverts and rump. The undertail has yellow feathers slightly cinnamon toward their bases; this cinnamon is lacking or barely hinted at in the *xanthopygus* specimens at hand. The rump feathers, basically yellow, show cinnamon at their bases, edges, and tips, definitely exceeding the variation within *xanthopygus*, but closer to that form than to *punctatus*. The white-spotting of the lower back seems unaffected by the cinnamon evident in nearby rump feathers. We conclude that this specimen represents a backcross product of a hybrid between *xanthopygus* and *punctatus* with *xanthopygus*.

Male, 5 km. south-southeast of Heywood (18.5 km. north-northeast of Portland), AMNH 824921. The voice of this male was recorded, and the bird taken at the edge of moist sclerophyll forest on November 24, 1979. It weighed 7.8 grams, and its testes measured 2 by 1 mm. Other pardalotes in the area included rusty-rumped and yellowish-rumped birds. Mensurally this specimen is within the range of overlap of both forms, except that it has a long bill (8.0 mm.), which may or may not reflect a tendency toward *xanthopygus*. The throat is golden yellow in this bird, less rich than in many *punctatus*, but within the range of variation of that form. Its underparts are a trifle pale cinnamon, but

this may reflect fading; it is too richly cinnamon for *xanthopygus*, and within the range of variation exhibited by *punctatus*. The yellow undertail coverts have richly cinnamon bases, as in *punctatus*. Its dorsal spotting is peculiarly variable, and as the bird is not moulting, this variation is important. A few feathers bear quite rusty spots, most are very faintly buff-tinted, and a few anterior back feathers bear almost white spots. Some faded, worn *punctatus* come close to matching this specimen in dorsal coloring, but none is so variable, and none has such pale anterior spotting. The rump color also is mixed, nearly chestnut at the tips of some feathers and paler cinnamon elsewhere with a hint of yellow. The rump feathers are worn and partly faded. The uppertail coverts barely show tipping of red-orange, not red, and the combination of this lack of red and the mixed coloring of the rump was what probably attracted our attention to it. Thus, the bird may be a hybrid or a backcross product (hybrid × *punctatus*), as indicated by its back and rump coloring (its long bill may be considered suggestive of such a cross, though not significant in itself).

Male, 4.3 km. southwest of Heathmere (12 km. north-northwest of Portland), National Museum of Victoria collection. On November 25, 1979 we obtained this bird, weighing 7.5 grams and with testes 2 × 1.5 mm. (right testis smaller, 1 by 1 mm.), in heathy, moist sclerophyll forest. Its vocalizations were tape-recorded (and proved identical in every way with those of *punctatus*). All its measurements are within the range of overlap between *punctatus* and *xanthopygus*. The specimen is quite richly colored, with golden yellow throat tinged cinnamon, richly cinnamon underparts, broadly cinnamon-based undertail coverts, buffy cinnamon back spotting (quite pale anteriorly, but matched by some *punctatus*), and rusty chestnut uppertail coverts. We have no hesitation in considering this bird to represent *P. punctatus*; others with chestnut rumps were seen in the surrounding forest.

#### SUMMARY OF MORPHOLOGICAL AND VOCAL DATA FOR THESE SPECIMENS

Combining results of the morphological comparisons and vocal data, we find: 1) the

Inglewood male morphologically is a likely hybrid with *punctatus*-like vocalizations that show some peculiarities, and we conclude that it is a likely hybrid or backcross product; 2) the Mitre male is mainly *xanthopygus*-like in morphology and in voice, but shows definite tendencies toward *punctatus* in both, hence we consider it a backcross product of a hybrid with *xanthopygus*; 3) the Heywood male is mainly *punctatus*-like in morphology and in vocalizations, but with peculiarities in both cases—we conclude that it represents a hybrid or the result of the crossing of a hybrid with *punctatus*; and, 4) the Heathmere male morphologically and vocally is *punctatus*-like (with some vocal peculiarities), and we assign it to *punctatus*.

#### DISCUSSION AND CONCLUSIONS

Of six calls described for these pardalotes, three (Fast Chip, Whee, Weet calls) are so far known only from *P. punctatus*, although approaches to the Whee and Weet calls have been noted above in *P. xanthopygus*. The special circumstances under which the Fast Chip Calls were recorded in *punctatus* suggest that they are uttered under similar circumstances in *xanthopygus*. Another call, the Begging Call, was recorded only from *xanthopygus*, but such calls are generally similar in congeneric species (e.g., of woodpeckers; Winkler and Short, 1978), and are apt to be similar in *punctatus* and *xanthopygus* and certainly to occur in *punctatus*. The Short Weep and Long Weep calls described for both species are alike in the case of the former call, and their Long Weep Calls differ only slightly. It thus appears likely that the six calls occur in both species, and that they are very similar if not in every case identical in the two. Data do not yet permit us to state that the calls are functionally identical, but we have no evidence to the contrary.

The songs of males of the two species differ in the form of their elements, their pitch, and their temporal features, although the general structure of the songs and their quality are similar. Both sing abbreviated versions of their respective songs, the context and function of which are not clear in relation to those of the full songs. The songs function in defense

of territory, both species being highly aggressive toward conspecific birds and toward other species as well (both are aggressively interactive with, and dominant over the sympatric *Pardalotus striatus*, despite the latter being larger than either *punctatus* or *xanthopygus*). The songs function probably in synchrony of reproduction and pair-bond maintenance between mated birds, judging from the great frequency of songs and "excited" behavior of singing males in the presence of their mates. Finally, the very often repeated songs clearly indicate the location of the singers to the mate, and to adjacent conspecific pairs.

The results we have presented concerning interbreeding of *P. punctatus* and *P. xanthopygus* require amplification and further study, especially in those areas in which these two pardalotes meet. Our vocal data are suggestive of at least limited hybridization between the Spotted and Yellow-rumped pardalotes. We emphasize the need for further study of the variation in vocalizations of both forms. Also, the ontogeny of the vocalizations and inheritance of various calls and songs require investigation. Nonetheless certain individual birds show vocal convergence, and they come from areas of contact or overlap between *punctatus* and *xanthopygus*. Most importantly the intermediacy we have described in vocalizations of some individuals is matched by their morphological intermediacy. This concordance of two diverse character systems and their occurrence of course strengthens our bases for believing that these pardalotes interbreed, although we must rely mainly on the morphological data until the vocalizations of the two are subjected to more intensive studies. This does not detract from the importance of the vocal data, which in themselves represent a significant advance in our knowledge of the behavior of pardalotes.

Sample sizes from areas of contact so far are insufficient to establish the incidence of hybridization between *punctatus* and *xanthopygus*. In particular, human modification of habitat may have limited or enhanced contact between the two in recent times, as Salomonsen (1961, p. 14) has suggested. Hence, not only are appropriate samples needed from central and western Victoria, southern South Australia and southwestern (Western) Australia, but the ecological situation in the areas

of sampling needs to be investigated concurrently.

The Spotted Pardalote has been assumed (e.g., Salomonsen, 1961; see also Keast, 1961) to be a Bassian (wet, southern Australian) derivative, and the Yellow-rumped Pardalote, an Eyrean (arid, interior Australian) derivative of their common ancestor, with spreading of both in a complicated manner to the west and to the east subsequent to speciation such that both taxa now have populations isolated in southwestern, south-central and southeastern Australia. Until we know more about the interactions of the two forms in all their areas of contact it seems premature to speculate on their history and we defer this until a later time.

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#### ADDENDUM

After completion of the manuscript Schodde, in his review of Australian pardalotes for the passerine portion of the Royal Australasian Ornithologists' Union Checklist, was able to study specimens at the various Australian museums. This study revealed evidence of some introgression, and hybridization between *P. punctatus* and *P. xanthopygus* from the Mt. Lofty and southern Flinders Ranges southeast through the lower Murray "Mallee" and the Ninety-mile Desert to western Victoria. For example, among 73 specimens from the South Australian Museum representing the area just mentioned no fewer than 49 blend the morphological features of both forms to varying degrees and in diverse combinations. This strongly supports the likelihood of hybridization as a causal factor for the vocal variation discussed herein.

That shifts in habitat and human-induced modifications of the environment account for some of the interbreeding is indicated by two

hybrids (in Australian National Wildlife Collection, Canberra) of *xanthopygus* and *punctatus* taken at Peebinga, South Australia, in May 1976; prior to 1950 only *xanthopygus* had been collected around Peebinga. The Spotted Pardalote frequents wetter, generally coastal eucalypt forests and woodlands, and the Yellow-rumped occurs in drier "mallee" woodland from the coast to farther inland. The areas where these habitats meet, interdigitate, or intergrade are precisely where the two pardalotes meet, and it appears that human factors (cutting of wetter forests and woodlands, and of mallee, forcing the birds to move elsewhere) are facilitating their contact.

Study of larger series shows a tendency for disparate sexual dimorphism in these pardalotes, for, whereas male and female *punctatus* are identical in their buffy back-spotting, female *xanthopygus* are more coarsely, more buffy and less white spotted than males. This fact and the duller, buffier rump of fe-

male *xanthopygus* suggest that buff coloring is the ancestral condition, which may imply the origin of *xanthopygus* from a more *punctatus*-like ancestor (following Gloger's Ecogeographic Rule).

Schodde notes that the Karoonda recordings of Swaby may have been from a hybrid *punctatus* × *xanthopygus* or been influenced by gene flow from *xanthopygus*, in view of the introgression he has only recently found to be widespread in the Murray Mallee.

The possibility must be considered (Schodde, in recent publications) that both species discussed herein are indeed Bassian in origin, with *punctatus* arising in the east and spreading west, and *xanthopygus* arising

from the same transcontinental stock in the west and spreading east.

Finally, very recent observations of singing male *punctatus* make it obvious that the song is indeed primarily territorial in function. Singing males use an uncluttered vantage point such as a bare twig just beneath the sheltering canopy of a small tree. There, they raise the body to an almost upright, stretching posture, crane the neck and tilt the head and bill slightly downward in voicing each song-phrase, twisting this way then that way as if to aim the signal in several directions, or to peer in different directions for a prospective challenger.

