Con e , S r c ral Variabili and Di inc i ene of California To hee (*Pipilo crissalis*) Vocal D e

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Paired bird prod ce ocal d et b coordinating o nd prod ction to prod ce a temporall and aco tically organi ed ignal (Thorpe 1972; Farab- a gh 1982). E i ting de nition , ho e er, allo a arie t of differen t ignal to be labeled 'd et '. D et tr c t re ar idel , and ma con i t of highl coordinated ong (like the d et of the plain ren; Mann et al. 2003) or imple o erlapped call (like the d et of the Carolina ren; Sh ler 1965) (Farab- a gh 1982). D et are all prod ced b mated pair , b t ma al o be prod ced b nmated male female pair (Roger 2005) or b other a ociating indi id al , ch a male male pair of manakin di pla ing to attract female (Trainer et al. 2002). A ed b ome pecie d ring join re o rce defen e and for ma e-g arding (Seib & Wickler 1977; Sonnen chein & Re er 1983). Se eral differen a pec of d e r c re ma inform o r nder anding of method follo ing Grif th et al. (1998). Thro gho t the co r e of the t d , indi id al ere re eighted opport ni ticall . Thirt - i indi id al ere inten- i el ob er ed d ring focal animal atche incl d- ing 218 h of ob er ation time bet een 31 Ma 2003 and 19 Apr. 2006. Watche began bet een 6:00 and 10:00 ho r , depending on tempera t re and nri e, and paired bird ere ob er ed on cce i e da .

D ring focal-animal atche , ob er er noted the location, habitat, beha ior and ocali ation of the focal California to hee e er 2 min. All interaction ith con peci c , incl ding ocal d et , ere noted. Re earcher ob er ing d et took nat ral hi tor note and ometime mea red d et lo dne ith a portable o nd le el meter (Radio Shack Model: 33-2055, Radio Shack, Fort Worth, Te a , USA). D et and olo q eal ere di ting i hed b ear, a ta k that i relati el ea hen ob er ing bird direct l (b t not hen e amining pectrogram) b a rall a e - ing the location of o nd prod ction. When both bird ere i ible, ob er er al o atched for mo e-ment of the bill and bod . An q eal ocali ation gi en b a ingle bird, not o erlapped temporall b a q eal ocali ation from another bird a con idered a olo. An q eal ocali ation gi en b t o bird that o erlapped temporall ere con idered d et .

California to hee q eal ocali ation e ent fre-q encie ere calc lated for 17 pair . Sq eal d et fre-q encie per pair ere calc lated a the total n mber of q eal d et ob er ed o er the total ob er ation time per pair. O erall q eal d et ocali ation fre-q encie are a erage of pair freq encie . Solo q eal freq encie per indi id al ere calc lated a the n mber of olo q eal ob er ed o er the total ob er-ation time for that indi id al. O erall olo q eal fre-q encie are calc lated a a erage of indi id al freq encie . We al o calc lated ong freq enc for mated and nmated male a the n mber of ob er a-tion inter al d ring hich a male a ob er ed ing-ing o er the total n mber of ob er ation inter al for all male in each categor . Mean rate of olo q eal ocali ation from male and female ere compared ing a t o-tailed St dent' t-te t.

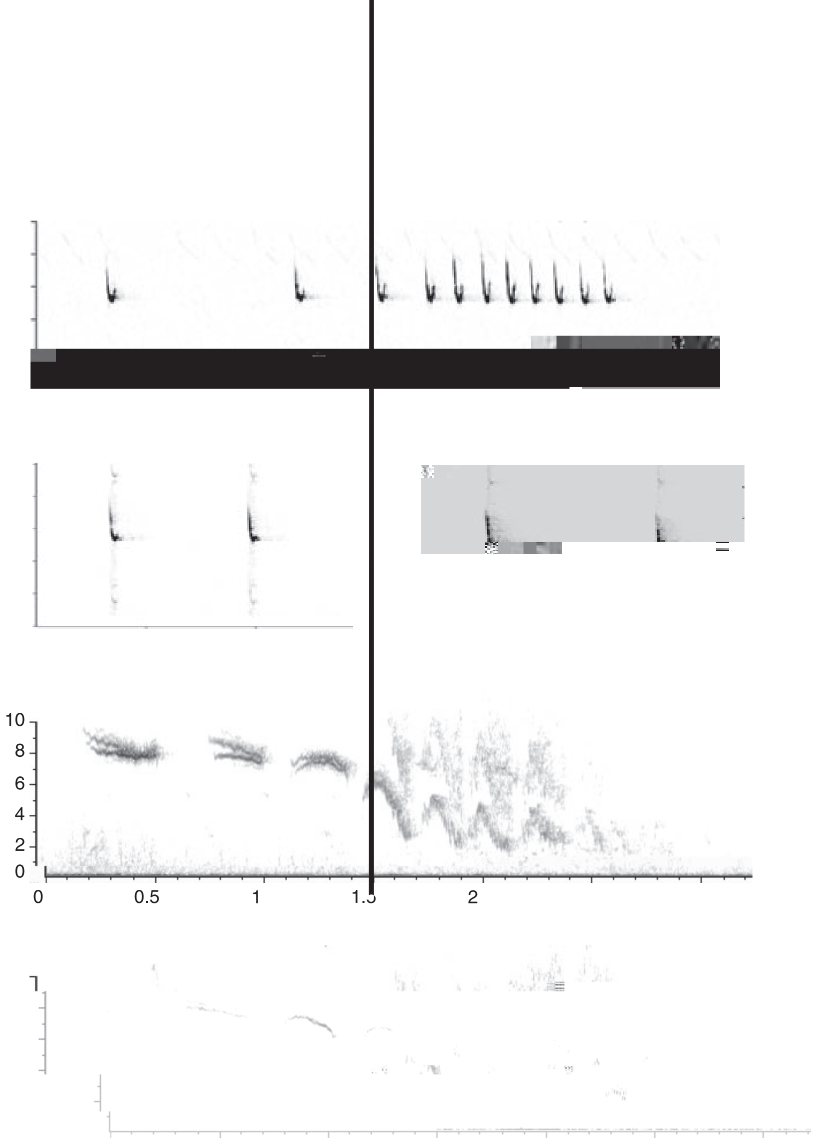
Acoustic Structure

Vocali ation tr ct re de cription and anal e are ba ed on a dio le recorded from the pop lation bet een 23 Ma 2003 and 19 Ma 2006. Re lt come from o er 400 h of recording time, and q alita-ti e de cription are ba ed on ob er ation of o er 30 pair . All recording ere made ith a Sennhei er MKH70 long hot g n microphone (Sennhei er, Wedemark, German) attached to either a Son TC-D5ProII ca ette recorder (Son , Tok o, Japan) or a Marant PMD670 compact a h digital recorder (Marant , Sagamihara, Japan). Ca ette recording ere capt red at a ampling rate of 22 kH and con- erted to digital le ing the program SYRINX (http:// rin pc.com). Digital recording ere made in mono at a ample freq enc of 48 kH and a bit-depth of 16, and ere tran ferred directl to a Dell PC for torage and anal i . Vocali ation ere con erted to pectrogram ing Ra en o nd anal i oft are (Ver ion 1.2; Cornell Laborator of Ornitholog , Ne York, USA) for characteri ation of pectral propertie .

To de cribe q eal ocali ation propertie e identi-ed three llable t pe (' q eak ', 'do n eep ' and ' q eal ') and one of (JM) mea red the follo ing ariable on- creen ith c r or rele ant to the entire ocali ation: n mber of q eak llable , n mber of do n eep llable , n mber of q eal llable , total

To te t for difference bet een pair e incl ded the ame 20 ariable from all 57 d et in a di crimi-nate f nction anal i (DFA). Thi anal i a e ed hether or not all d et from each pair are cla i -able a member of a ingle gro p niq e to that pair. Beca e ample i e aried among pair , e bjected thi DFA to chance correction (Tit et al. 1984). We al o performed a DFA on the 14 olo q eal from a paired male and female in order to determine if e co ld acc ratel a ign each q eal to an indi id al.

O r third te t of d et di tincti ene e amined the imilarit of the introd ctor q eak note acro and ithin pair . Mate freq entl join d et after hearing onl q eak note from the initiating part-ner, o e h pothe i ed that the e llable are likel to contain ignat re of identit . To te t the di tincti ene of q eak llable , e ed the oft-are program SOUND ANALYSIS PRO (Tchernicho ki et al. 2000) to calc late imilarit al e for compar-i on of pair of q eak llable . Thi program e a m lti-taper pectral anal i method and ha been ho n to be highl effecti e at cla if ing bird o nd to partic lar pop lation (analogo to indi-id al in o r t d) (Baker & Log e 2003). Thi anal i incl ded 60 d et from nine pair . Before performing imilarit anal e , the r t q eak lla-ble a cropped from each d et, lea ing no lead-in or follo time and a ed a a eparate o nd le. U ing the program RAVEN, freq encie belo 6 kH and abo e 10 kH ere ltered o t to remo e potential confo nding effect of backgro nd noi e. In a minorit of le , ob io remaining backgro nd



appear a fairl moo th de cending la he acro a ide freq enc range. Sq eal ocali ation recorded from the t d pop lation contained bet een 0 and 8 do n eep llable , ith a median of onl 1. Sq eal llable are trill containing a erie of er brief de cending note (each one la ting appro i-matel 0.02) that together form a q eal-like noi e. Sq eal ocali ation contained bet een 0 and 31 di tinct q eal llable , eparated b pa e . In man ocali ation , do n eep grade eamle l into q eal , and the t o o nd ma appear a part of a ingle, temporall contin o llable (Fig. 1d,e). Sq eal ocali ation propertie and lla-ble propertie are mmari ed in Table 1.

D et are al a compo ed of the q eal ocali a-tion, b t do not ha e perfectl con i tent tr ct re or timing. Bird ar the n mber of each llable t pe in d et and al o timing ith hich the re pond to the q eal of their partner (Table 1). D et contrib tion from t o partner are al a o erlapping b t not identical or im ltaneo (Fig. 2).

Vocalization Use

Paired bird prod ced all d et ith their partner and nmated bird ere ne er heard to q eal. The majorit of q eal ocali ation prod ced b focal animal d ring ob er ation ere ed in d et , rather than olo . In 218 h of ob er ation time, 95% of all q eal ocali ation ob er ed ere gi en a part of d et . Pop lation- ide ocali ation rate ere 3.0 ± 2.29 d et per ho r per pair and 0.28 ± 0.40 olo per ho r per indi id al. Male prod ced olo q eal at a rate of 0.38 ± 0.54 per ho r, hile female prod ced 0.19 ± 0.20 per ho r. The e rate are not tati ticall di ting i hable (t_{28} = 1.30, p = 0.21). Additional ob er ation indi-cate that California to hee d et thro gho t the ear, b t rate pre ented here appl onl to the pring breeding ea on bet een 15 Mar. and 25 J l. bet een 6:00 and 12:00 ho r .

Sq eal d et ere performed at a range of ol- me , ometime a lo d a 55 60 dB (mea red at a di tance of 5 m), and ometime o oftl a to be almo t ina dible to a per on at a di tance of 5 m. Focal bjects d etted a infreq entl a once in a 2-h ob er ation period and a freq entl a 15 time in an ho r of ob er ation. D et ere ometime prod ced in relati el rapid cce ion, p to a ma - im m of e time in a min te. All d et occ rred bet een mated pair of California to hee . In a fe in tance , indi id al appeared to direct q eal ocali ation at chick , b t thi al a occ rred in den e egetation here a mate ma ha e been pre ent.

Both male and female initiated d et and both e e joined d et a the econd partner to ocali e. Male and female q eal ocali ation ere imilar eno gh that the ere indi ting i hable to h man li tener . Male and female beha ior ere al o apparentl identical hile d etting. Ob er er ere onl able to differentiate male and female bird per- forming d et ba ed on band combination .

Sq eal d et ere al a a ociated ith a tereo- t ped approach beha ior bet een mate . Bird began ocal d et in a ariet of location , ome- time eparated b di tance of o er 10 m and i al ob tr ction , b t ne er concl ded d et ntil the t o pair member ere po itioned right ne t to each other (al a ithin 1 m) and ere in i al con- tact. Not onl bird po itioned clo e together b t bird po itioned far apart al o began q eal d et reg larl . D et bet een patiall eparated bird eigen al e abo e 1, all of hich indicated little pair di tincti ene . An anal i of ariance for PC-1 did nd that ome pair had igni cantl different mean ($F_{7,56} = 2.76$, $p = 0.017$), b t the range of PC-1 al-e o erlapped for all pair . St dent' t-te t indicated that no ingle pair had a mean di tinct from all other pair mean al e . Similarl , an anal i of ariance for principal component 2 (PC-2) fo nd that ome pair had igni cantl different mean al e ($F_{7,56} = 3.40$, $p = 0.005$), b t St dent' t-te t again re ealed that no ingle pair had a mean di tinct from all other pair mean al e .

Di criminant f nction anal i cla i ed 91% of d et to the correct pair. For e pair all d et ere cla i ed correctl , and the remaining three pair had either one or t o of their d et mi cla i ed to the rong pair. Altho gh ample i e aried b pair, chance correction indicated that thi re lt a d e to a good model t (K = 0.90).

Similarit anal e performed on 60 d et from nine pair (6.7 ± 2.2 per pair) indicated that q eak are p rel indi id al- or are e -ba ed. The d et of man other pecie ha e markedl different male and female part , and e en hen male and female prod ce imilarl   tr ct red d et contrib tion , re earcher ha e fo nd that indi id al gi e ocali a-tion   ith non-o erlapping aco tic trait (Mann et al. 2003; Roger 2005; Seddon & Tobia 2006; Wright & Dahlin 2007). The imilarit of California to hee d etting beha ior and ocali ation propertie from male and female i remarkable and ho ld limit, b t not nece aril e cl de, e recognition ba ed p rel on q eal ocali ation . The imilarit of male and female q eal ma indicate that the important ignal content of d et i not the e of each bird, b t the fact that t o paired indi id al are pre ent and the identit of tho e indi id al . Thi information o ld be mo t al able nder h pothe-e that gge t cooperati e f nction of d etting, ch a re o rce defen e or ignaling partner location and commitment (Hall 2004).

A   ith olo q eal , there i great ithin-pair ariabilit in d et characteri tic . Ne erthele , anal- e of both entire d et and j t the introd ctor   q eak indicated that the e ocali ation pro ide information abo t identit . Beca e d et are al a performed b mate on their o n territor , location ma al o pro ide cl e abo t d etter identit . Sepa-rate anal i of d et contrib tion b indi id al bird   o ld pro ide more information on thi topic, b t nfort natel it i impo ible to eparate male and female d et contrib tion in a dio recording or pectrogram . Ne erthele , if indi id al prod ce di tincti e q eal ocali ation , then difference bet een pair   ho ld be mea rable. E perimental te t of q eal recognition   ing ocali ation pla -back   o ld al o be highl informati e b t dif c lt, if not impo ible, to do among California to hee   here male and female d et contrib tion cannot be eparated. In the ab ence of   ch e perimental te t , ocali ation mea rement data pro ide the be t po ible information abo t the potential for indi id al or pair recognition. California to hee are one of the fe   pecie to be t died in depth   here male and female prod ce the ame d et ocali a-tion t pe. B e amining thi   niq e o nd e add to the e i ting nder tanding of the di er it of a ian ocal d et .

The d et of California to hee ho far le pair di tincti ene   than do d et of other pecie in hich aco tic propertie and e en phra ing ma   ar con iderabl bet een pair (Mann et al. 2003; Log e 2006; Seddon & Tobia 2006). It i   nclear h   q eal ocali ation are o highl   ariable, b t po ible that pla ticit in d et prod ction ma better allo pair to adapt their ocali ation to a ariet of it ation . For e ample, a the d et i al a a ociated ith a ph ical approach beha ior, d et ill ar in d ration according to the amo nt of time it take for the pair to approach each other. Change in   llable n mber and length therefore, might re ect the di tance bet een bird at the tart of the d et. Ob er ation incorporating conte t al information   ith d et tr ct re   o ld be highl informati e in helping to make en e of thi   tr c-t ral di er it .

California to hee d et tr ct re pro ide in ight

Ak m A

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