DUSTBATHING IN BOBWHITE QUAIL (COLINUS VIRGINIANUS): A REGULATORY MODEL

Thesis for the Degree of Ph. D. MICHIGAN STATE UNIVERSITY PETER L. BORCHELT 1972



This is to certify that the

thesis entitled

DUSTBATHING IN BOBWHITE QUAIL (COLINUS VIRGINIANUS): A REGULATORY MODEL

presented by

PETER LEE BORCHELT

has been accepted towards fulfillment of the requirements for

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ABSTRACT

DUSTBATHING IN BOBWHITE QUAIL (COLINUS VIRGINIANUS):

A REGULATORY MODEL

BY

Peter L. Borchelt

Dustbathing is one of a variety of biologically adaptive behaviors associated with care of the body surface which occur in a large number of avian species. Descriptions of dustbathing in many species are available, but few experimental investigations of this behavior have been reported. Borchelt, Eyer and McHenry (in press) briefly described the components of dustbathing in Bobwhite quail (Colinus virginianus) and reported that the frequency of some of the components showed systematic increases with deprivation of dust. It was also observed that the feathers of birds which were deprived of dust had a more "oily" appearance than those of birds which had just dustbathed. A lipid regulation model was proposed for the function of dustbathing which stated that lipids from the uropygial gland were deposited on the feathers through "oiling" behavior to insure adequate lubrication of the feathers for maintenance of body temperature and for flight (Simmons, 1964). When the amount of lipids exceeds a critical level, the bird dustbathes. Dustbathing serves to remove lipids by driving dust into the plumage, after which the dust and lipids are vigorously shaken out of the plumage.

The present experiments were designed to 1) describe in detail the organization of components of the dustbathing sequence in Bobwhite quail, and 2) test the proposed lipid regulation model by determining whether the amount of lipids on the feathers changes with deprivation of dust and whether surgical removal of the uropygial gland leads to a decrease in frequency of dustbathing.



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In experiment 1, the frequencies of all of the components of the dustbathing sequence of each of 24 Bobwhite quail (housed in male-female pairs) were recorded, twice at 1 day of deprivation of dust, and for 18 of the birds, once at 5 days of deprivation. The two tests at 1 day of deprivation provided a measure of reliability of frequencies of components and the test at 5 days assessed the effects of an increase in deprivation on the frequencies of all components.

The results showed that the frequencies of some of the components, and the sequence of first occurrences of the components, were highly reliable. The frequencies of some of the components were also highly intercorrelated, and the probable sequence of the first occurrence of components revealed a high degree of stereotyping for some components. Significant changes occurred in the frequency of many of the components with deprivation of dust, and two of the components showed sex X deprivation interactions. The conditional probabilities of some components exhibited time trends, and considering all occurrences of each component revealed a high degree of variability between birds in order of components. These results are discussed in relation to the classic definition of the fixed, or model action pattern, and in terms of the analysis of behavioral sequences into appetitive, consummatory and post-consummatory components.

In experiment 2, 4 groups of Bobwhite quail were housed in groups of 9-13 and deprived of dust for either 1, 5, 15 or 180 days. After the appropriate deprivation period, the birds were sacrificed and a standard ether extraction procedure was used to assess the amount of lipids on a 2-3 gm. sample of the feathers of each bird in each group. The r

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The results showed a significant increase from approximately 5 mg. of lipids per gm. of feathers at 1 day of deprivation, to 15 mg. at 5 days, to 35 mg. at 180 days of deprivation. These results strongly support the lipid regulation model which predicts a change in amount of lipids on the feathers with deprivation of dust.

In experiment 3, 7 pairs of birds were divided into three groups. An experimental group (3 pairs) had the uropygial gland surgically removed while a sham-operated control group (2 pairs) recieved an incision on the back. Two pairs of birds formed an untouched control group. Starting one week after the experimental manipulations, the birds in all groups were given three tests at 1 day of deprivation at weekly intervals. These birds second test at 1 day of deprivation in experiment 1 served as a baseline to assess post-operative changes. In brief, no systematic changes between the baseline and any of the three post-operative tests were evident in any of the three groups. The possible addition of an "experience" factor to the lipid regulation model is discussed.

These three experiments begin experimental analysis of a care of the body surface behavior which occurs in a wide range of species. Further research investigating variables affecting dustbathing will lead to refinement of the lipid regulation model and may provide sufficient information to explicate the relations between the variety of behaviors associated with care of the body surface and yield a comparative analysis of this biologically important class of behavior.

Signed:

DUSTBATHING IN BOBWHITE QUAIL (COLINUS VIRGINIANUS): A REGULATORY MODEL

BY

Peter L^{e^C} Borchelt

A THESIS

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Department of Psychology



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iii

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TABLE OF CONTENTS

List of Tables	V
List of Figures	VI
General Introduction	1
Experiment 1	8
General Discussion	38
Experiment 2	44
Experiment 3	51
General Discussion	57
References	60
Appendix	63

Tat 1

2

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LIST OF TABLES

Table		Page
1	Means, standard deviations and ranges of frequencies of test 1 components, and corre- lation coefficients (Pearson product moment) between frequencies of components of test 1 and test 2 (N = 24).	15
2	Intercorrelations (Pearson product moment) among the frequencies of components.	16
3	The average probabilities of first occurrences of components in relation to other components for test 1.	21
4	The average probabilities of first occurrences of components in relation to other components for test 2.	22
5	The average probabilities of first occurrences of components in relation to other components for test 3.	23
6	A comparison, between subsequences, of the median conditional probabilities (+ quartile deviation (Q)) associated with the occurrences of components.	26
7	A comparison of predictability of models I and II.	- 3
8	A time course of values of $F_N^{}$, $O_N^{}$, and $D_N^{}$ for models I and II.	75

±00.753

LIST OF FIGURES

Figure		Page
1	An illustration of the lipid regulation model.	6
2	An illustration of some components of dustbathing in Bobwhite quail.	12
3	Mean frequency (<u>+</u> standard error) of dustbathing components at one (test 2) and five (test 3) days of deprivation.	18
4	The sequence of components and conditional probabilities associated with transitions between components (male number 1, test 1).	28
5	The sequence of components and conditional prob- abilities associated with transitions between components (female number 1, test 1).	30
6	The sequence of components and conditional prob- abilities associated with transitions between components (male number 2, test 1).	32
7	The sequence of components and conditional prob- abilities associated with transitions between components (female number 8, test 2).	34
8	The sequence of components and conditional prob- abilities associated with transitions between components (male number 4, test 1).	36
9	Mean amount (+ standard deviation) of lipids on the feathers of birds deprived of dust for 1, 5, 1 or 180 days.	.5 , 46
10	Mean number (+ standard error) of dust tosses, hear rubs, and side rubs during the baseline and the three post-operative tests.	ıd 54
11	An illustration of the original lipid regulation model.	64

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GENERAL INTRODUCTION

Although dustbathing is a behavior that occurs in a wide variety of avian species, it has received relatively little experimental investigation. General references to care of the body surface in birds (e.g. Simmons, 1964; Goodwin, 1956) mention dustbathing and describe the general sequence of behaviors involved.

Simmons (1964) described this general sequence as follows: "Most dusting species form hollows of dust, if conditions allow, by squatting or lying down and performing movements of the bill (flicking, pecking), feet (scraping), and body (shuffling, rotating). The dust is driven into the plumage, either directly or indirectly, by movements of the wings (flicking, shuffling, shaking), or feet (scratching as in nest shaping or with one foot only), or of both wings and feet, the bird relaxing or ruffling its contour feathers, especially those of the rump, and often rubbing the head and bill in the dust. After dusting proper, the earth is shaken out of the plumage, often vigorously."

The usual medium for dustbathing is fine, dry earth, sand, or possibly dry rotten wood, although one report mentions observations of House Sparrows dustbathing in sugar (Goodwin, 1963).

Speculations concerning the evolutionary origins of dustbathing have attempted to relate dustbathing to other care of the body surface behaviors. Chisholm (1944) postulated that dustbathing is the behavior from which anting was derived. Anting consists of movements whereby

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the defensive and other body fluids of ants (Formicidae) are applied to the birds feathers (Simmons, 1964). This explanation was discounted by Simmons (1957) on the basis that anting and dustbathing behaviors differ in form. Another speculation, by Nicolai (1962) states that dustbathing probably evolved from water bathing. Dustbathing has also been used in attempts to clarify phylogenetic relationships, for instance, between species of <u>Columbidae</u> by Nicolai, and <u>Motacillidae</u> by Mester (1969), but without great success. Before phylogenetic comparisons can be fruitfully attempted and relations between care of the body surface behaviors discovered, research first has to be conducted focusing on the earlier stages of the comparative method (Denny and Ratner, 1970), which include precise description of behaviors, identification of productive preparations and explication of variables affecting the behavior of interest.

A few studies have investigated variables affecting dustbathing in birds. Benson and Schein (1965) found that particulate surfaces (sawdust, soil, sand) elicited more dustbathing than solid surfaces (glass) in <u>Coturnix</u>, but the color of the substrate did not influence the incidence of dusting. Variations in air temperature and relative humidity did not significantly affect the incidence of dustbathing. Also, birds exhibited a "satiation" effect, that is, birds maintained on a sawdust floor dustbathed in sawdust less than birds maintained on a wire floor.

The effect of age of the bird on dustbathing has been investigated in <u>Coturnix</u> chicks (Brett & Kruse, 1967), White Rock chicks (Nice, 1962), and Burmese Red Jungle fowl chicks (Kruijt, 1964); these studies

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A recent study by Borchelt, Eyer and McHenry (in press) briefly described the sequence of components of dustbathing in adult Bobwhite quail and found that deprivation of dust affected the frequencies of some of the components. The components of the dustbathing sequence include preliminary pecking and scratching movements in the dust, squatting in the dust, movements of the wings and feet to toss dust onto the birds' ruffled plumage (dust toss), rubbing the head and side in the dust (head rub and side rub), and ruffling of the feathers and shaking the dust out of the plumage (ruffle-shake). The sequence of components generally occurred in this order, although the precise order of the various components was quite variable. One aspect of the sequence was found to be highly stereotyped. After initial pecking, scratching, and squatting components, one or more dust tosses always occurred before the first head rub. In turn, one or more head rubs always occurred before the first side rub. No changes in the sequence of components were observed with an increase in deprivation of dust from 1 to 5 days.

The frequencies of some components, however, increased significantly with an increase in deprivation level. The frequency of dust tosses and head rubs increased from 1 day to 5 days of deprivation, while the increase in frequency of side rubs, the decrease in latency to enter

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the dust, and the difference in median numbers of seconds between successive dust tosses approached statistical significance. No differences were found in the frequencies of components between male and female birds.

Deprivation, then, is an important variable affecting some components of dustbathing, as it is for components of other classes of behavior, such as eating, drinking, and sexual behavior. This suggests that dustbathing functions as a regulatory system, with deprivation of dust leading to changes somewhere within the system, consequent feedback, and resulting compensatory changes in behavior. Borchelt, et al. suggest that the mechanism underlying such a system for dustbathing is regulation of lipid substances on the birds' plumage. They observed that birds deprived of dust for 5 days had a more "oily" appearance than birds which had just dustbathed. Healy and Thomas (personal communication) have observed that Japanese quail (<u>Coturnix</u>) also have an "oily" appearance when deprived of sawdust for dustbatning.

There are two sources of lipid on the plumage of birds. The feathers themselves contain endogenous lipid (from one to three per cent by weight depending on the species), probably as a by product of keratinization, a process occurring during the development of the feather (Bolliger and Varga, 1960). In addition, lipid material from the preen or uropygial gland is applied to the surface of the feathers. This 'oiling" behavior insures adequate water proofing of the feathers, maintenance of insulation, reduction of wear and chances of breakage, and possibly provides a source of vitamin D (Simmons, 1964). If some species of birds regulate the amount of lipid material on the feathers,

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a first approximation of how it might be accomplished is shown in Figure 1 (which is a simple non-linear regulatory mechanism; see Appendix 1 for details). "Oiling" behavior is assumed to continue at a constant rate, but when the amount of lipid increases above some critical level, (μ) the bird dustbathes. Dustbathing presumably removes lipid from the plumage when the lipid is absorbed by the dust during the dust toss, head rub, and side rub components, and is shaken out of the plumage during the ruffle-shake component. It is assumed that the bird can either discriminate (by some unknown sensory mechanism) the amount of lipid on the feathers, or it can monitor the amount of its "oiling" behavior to determine the amount of lipid on the feathers.

This lipid regulation model can be tested in a number of direct ways. If lipid from the uropygial gland elicits dustbathing, then the increase in dustbathing with deprivation of dust should be explained by an increase in lipid on the feathers with deprivation. Also, if the only source of additional lipid, the uropygial gland, is surgically removed, then the frequency of dustbathing behavior should decrease.

Three studies were designed to describe more clearly the dustbathing behavior of Bobwhite quail and to test the proposed lipid regulation model for the function of dustbathing. The first study will provide a detailed description of the dustbathing sequence under two conditions of deprivation of dust. The second study will determine whether changes in lipid on the feathers occurs with deprivation of dust, and the third study will investigate the effects on dustbathing following surgical removal of the uropygial gland.

Figure 1.--An illustration of the lipid regulation model.



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EXPERIMENT 1

Introduction

The first step in the analysis of behavior is a precise description of the behavior of interest (Denny and Ratner, 1970). This descriptive process includes subdivision of the behavior into recordable units or components and analysis of how the units are structured to form a behavioral sequence. Most analyses of behavioral sequences have been conducted on social behaviors, or behaviors which have some signal, or communication function. These analyses yield, for instance, flow diagrams of the courtship behavior of the fish <u>Badis badis</u> (Barlow, 1962), or of agonistic behavior of goldfinches (Hinde, 1955-1956). More complex analyses of communication behaviors are discussed by Altmann (1965).

Among non-social or non-signal behaviors, a few analyses have been made on sequences of care of the body surface (COBS) behaviors. Methods for describing sequences of COBS behaviors range from verbal descriptions of a variety of COBS behaviors in birds (Simmons, 1964), to transition matrices of components of washing and sandbathing behaviors of some <u>Heteromyid</u> rodents (Eisenberg, 1963), to auto- and cross correlations, intensity functions, and spectral functions of measures of components of maintenance behaviors of skylarks, <u>Alauda</u> arvensis (Delius, 1968).

Some major statistical and behavioral considerations limit the validity of some of these methods as they have been used. First,

previous studies attempting statistical descriptions of COBS behaviors have not considered individual differences in behavior. Sequences of behavior have typically been recorded from a number of different animals at different times and analyses made on the pooled data. Such analyses reveal, for instance, the probability that behavior A is followed by behavior B, C, or D, but give no indication of the amount of variability between different members of a species. A related question is how stable are the individual differences that occur.

A second question, dealt with in a few studies, is how the behavioral sequence is modified by either peripheral or central variables. For instance, Delius (1968) found that the frequency of maintenance activities of Skylarks is affected by seasonal and diurnal changes, as well as differing between males and females. It is important to determine both the inherent variability of behavioral sequences as well as the extent to which external variables modify the sequence if adequate classification of behavior is to be obtained or if "behavioral models" are to lead to discovery of central nervous system correlates (Denny and Ratner, 1970; Barlow, 1968).

The present study is designed to add detail to the verbal description of the sequence of dustbathing components offered by Borchelt, et al., (in press). The main questions asked include: 1) Do stable individual differences in the frequencies and sequence of the components occur? 2) Are the frequencies of some components of the sequence correlated with the frequencies of other components? 3) Is the sequencing of some components more stereotyped than the sequencing of other components? 4) What changes occur in the frequencies of all of the components, and in the sequence, with deprivation of dust?

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Methods

Subjects and Apparatus

The subjects used were twelve male and twelve female Bobwhite quail (Colinus virginianus) approximately 7 months of age. The birds were part of a colony obtained as chicks from the Department of Poultry Science. The colony was housed in groups of 8-12 birds in cages 137 x 50 x 30 cm. from the age of 1 to 5 months. During this time, food and water were continuously available and the birds had access to dust on an irregular schedule of 2-4 days per week. Dust consisted of dry earth sifted through a .6 mm. wire mesh screen. At the age of 5 months, twelve randomly selected pairs (one male, one female) were transferred to cages 70 x 40 x 30 cm. The birds were placed in male-female pairs to reduce the amount of fighting that occurs in sexually mature Bobwhite quail. Food and water were continuously available and dust was available on an irregular schedule of 2-4 days per week. The birds were maintained at all times on a 14-10 light-dark cycle (lights on at 0800) at $25(+1)^{\circ}$ C.

Observations were made from behind a one-way mirror mounted in the door of the housing room. Each component of the entire dustbathing sequence of each pair of birds was recorded by two experimenters (one experimenter per bird) on a two-channel Wollensack taperecorder. The recording experience of both experimenters consisted of recording dustbathing components during the Borchelt, et al. study and several hours of practice prior to the present study. The sequence of components for each bird was later transcribed onto data sheets for analysis.

Procedure

All tests were conducted in the home cage between 11:00 a.m. and 12:30 p.m. Each pair of birds received two tests at one day of deprivation and nine of the pairs received one test at 5 days of deprivation. A week elapsed between each test. Previous research (Borchelt, et al.) in press) had shown no order effect between 1, 3 and 5 days of deprivation in the frequencies of some dustbathing components when one day of access to dust separated different deprivation levels. In the present experiment, at least two days of access to dust separated each deprivation period which obviated the necessity of counterbalancing the one and five day periods of deprivation.

The test for each pair of birds consisted of inserting the dust tray into the cage after the scheduled deprivation period, closing the door of the housing room, observing through the oneway mirror, and recording the entire sequence of dustbathing behavior onto the taperecorder as each component occurred. Only the first dustbathing bout, defined as ending when 5 minutes elapsed without any dust tosses, head rubs, or side rubs, was recorded. The following dustbathing components, some of which are illustrated in Figure 2, were recorded: Entry into the dust tray, Scratch and Peck while standing, Squat, Scratch and Peck (Fig. 2A) while squatting, Dust Toss (2B), Head Rub (2C), Side Rub (2D), Rise, Exit the dust tray, Ruffle-shake (2E, F), and Other (eat, or drink). Preening was not recorded in the other category since preening did not occur very frequently during the dustbathing sequence.
Figure 2.--An illustration of some components of dustbathing in Bobwhite quail.

Results and Discussion

Every bird engaged in at least one dustbathing sequence on each test. The results of these three tests will be presented in two sections. The first section will include analyses made on the frequencies of components, while the second section will include analyses made on the sequences of components.

Frequencies of Components

Table 1 shows that large individual differences occurred in the frequencies of each of the components of dustbathing. The test-retest correlation coefficients of the frequencies of all of the components were positive and some were statistically significant. The three components actually involved in getting dust onto the plumage (dust toss, head rub, side rub) all had highly significant correlation coefficients, indicating stable individual differences in these components. It is interesting that pecking is the only one of the preliminary components which was highly reliable. This may be due to its inclusion as a component in a variety of other consummatory behaviors (e.g. eating, drinking, fighting). The significant correlation coefficients for the enter, exit, and other (eat, drink) components are presumably indicative of stable individual differences in general activity. No consistent differences were noted between the correlation coefficients of male and female birds.

Table 2 shows the correlation matrices among the frequencies of the components whose reliability coefficients were significantly greater than zero (peck while standing, peck while squatting, dust toss, head rub, and side rub), for tests 1, 2 and 3. The intercorrelations between

Means, standard deviations and ranges of frequencies of test 1 components, and correlation coefficients (Pearson product moment) between frequencies of components of test 1 and test 2 (N=24).

Behavior	Mean	S.D.	Range	r
Enter	4.8	5.0	1-25	.61**
Scratch	7.3	7.3	0-28	.31
Peck	15.3	18.6	0-71	.72***
Squat	5.1	2.7	1-15	.29
Scratch	9. 8	6.8	1-29	. 38
Peck	101.2	57.9	16-209	• 70***
Dust Toss	25.4	12.1	6-45	.66***
Head Rub	54.8	39.9	1-154	.69***
Side Rub	65.8	73.2	0-240	• 56***
Rise	5.0	2.7	1-15	. 30
Exit	4.3	5.2	1-25	•63**
Ruffle-Sha	ke 3.5	1.8	1-7	• 38
Other	1.8	1.3	0-5	.47*

* = p <.05 ** = p <.01 *** = p <.001 H

Intercorrelations (Pearson product moment) among the frequencies of components

			Test 1			
		Peck (Stand)	Peck (Squat)	Dust Toss	Head Rub	Side Rub
Peck	(Stand)		.26	51	41	42
Peck	(Squat)			. 34	.21	.52
Dust	Toss				.86	.69
Head	Rub					. 38

Test 2

	Peck (Stand)	Peck (Squat)	Dust Toss	Head Rub	Side Rub
Peck (Stand)		.12	40	35	28
Peck (Squat)			•66	.51	.51
Dust Toss				.72	.72
Head Rub					.84
			~ ~		

N = 24; .63 = p < .001; .52 = p < .01; .48 = p < .02; .41 = p < .05 For first significance test.

	Peck (Stand)	Peck (Squat)	Dust Toss	Head Rub	Side Rub
Peck (Stand)		.42	.22	.03	18
P eck (Squat)			.73	.47	.50
Dust Toss				.79	.74
Head Rub					.74

the frequencies of the dust toss and head rub components, and the dust toss and side rub components are highly significant (p < .001) for all three tests. The intercorrelations between the frequencies of the head rub and side rub components are highly significant (p < .001) for tests 2 and 3, but not significant for test 1. The high intercorrelations between these three components suggests that they serve common functions. The intercorrelations between pecking (either while standing or squatting) and these three components are more variable, although generally pecking while standing seems to be negatively correlated with the dust toss, head rub, and side rub components. The relations between pecking while squatting and these components may be due to the necessity of the bird to peck to loosen the dirt sufficiently for these components to occur.

There were changes in the frequencies of some of the components between 1 and 5 days of deprivation. Figure 3 presents the mean frequency (+ standard deviation) of each of the components for the 9 pairs of birds that were tested at each deprivation level. A two factor (sex X trials) analysis of variance with repeated measures on one factor (trials) (Winer, 1962) was computed for each of the components. No significant differences were found between sexes or over trials for the preliminary scratch and peck components. No significant difference was found between sexes for the squat component, but the frequency increased significantly (F = 12.38, df = 1, 16, p < .01) from 1 to 5 days deprivation. As would be expected, the same results were obtained for the rise component (F = 12.51, df = 1, 16, p < .01). No differences were found for the scratch while squatting component,

Figure 3.--Mean frequency (+ standard error) of dustbathing components at one (test 2) and five (test 3) days of deprivation.



but the frequencies of the peck while squatting (F = 22.07, df = 1, 16, p < .01) and the dust toss (F = 32.46, df = 1, 16, p < .01) components increased significantly with deprivation. The frequency of both the head rub and side rub components increased over trials (F = 27.78, df = 1, 16, p < .01; F= 24.18, df = 1, 16, p < .01, respectively), but, in addition, both of these components showed a sex X deprivation interaction, with males showing more of an increase than females (head rub, F = 4.64, df = 1, 16, p < .05; side rub, F = 4.36, df = 1, 16, p < .06). The frequency of the ruffle-shake component increased significantly with deprivation (F = 24.72, df = 1, 16, p < .01). The increase in the frequencies of both the exit and other component approached statistical significance, and the frequencies of the enter component at each deprivation level almost exactly mirrored the frequencies of the exit component.

Sequence of Components

A measure of the reliability of the sequence of components was devised by listing for each bird the order of the first occurrence of each of the components. Each component had been assigned a number from 1 to 13. Components missing from a birds' sequence were assigned the mean value of the components listed and included at the end of the list for that bird. This procedure was followed for the sequence of each bird at each test and yielded a very conservative measure of the test-retest reliability of the order of occurrence of components for each bird. The correlation coefficients thus computed between tests 1 and 2 ranged from .36 to 1.0 with a mean of .84.

Another representation of the structure of the sequence of components is depicted in Tables 3, 4 and 5. These tables show the average

The average probabilities of first occurrences of components in relation to other components for test 1.

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Enter	1	I	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Scratch	2	0	I	.55	.95	.95	.95	.95	1.0	1.0	.95	.95	1.0	.95
Peck	e	0	.45	I	.90	.90	.95	.95	.95	.94	.95	.90	.95	.89
Squat	4	0	.05	.10	I	1.0	1.0	1.0	1.0	1.0	1.0	.92	1.0	.90
Peck	S	0	.05	.10	0	t	.50	.71	1.0	1.0	.83	.92	1.0	.90
Scratch	9	0	.05	.05	0	.50	I	.79	.96	1.0	.87	.92	.96	.90
Dust Toss	٢	0	.05	.05	0	.29	.21	ı	1.0	1.0	.71	.92	1.0	.90
Head Rub	80	0	0	.05	0	0	.04	0	I	1.0	.52	.83	.91	.90
Side Rub	6	0	0	• 06	0	0	0	0	0	I	.50	.75	.85	.88
Rise	10	0	.05	.05	0	.17	.13	.29	.48	.50	I	.92	1.0	.90
Exit	11	0	.05	.10	.08	• 08	. 08	.08	.17	.25	• 08	I	.70	1.0
Ruffle-Shake	12	0	0	.05	0	0	•04	0	60.	.15	0	• 30	I	.80
Other	13	0	.05	.11	.10	.10	.10	.10	.10	.12	.10	0	.20	I

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The average probabilities of first occurrences of components in relation to other components for test 2.

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			Ч	7	e	4	Ś	9	٢	8	6	10	11	12	13
	Enter	-	I	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
	Scratch	7	0	ı	.55	1.0	1.0	1.0	1.0	1.0	1.0	1.0	.95	1.0	•94
	Peck	e	0	.45	I	.86	.91	.91	.91	.90	.90	.86	.77	.95	.88
	Squat	4	0	0	.14	I	1.0	1.0	1.0	1.0	1.0	1.0	.75	.95	.84
	Peck	S	0	0	60 .	0	I	.79	.75	1.0	1.0	.87	.71	.95	.84
F	Scratch	9	0	0	60.	0	.21	ı	.75	.91	1.0	.83	.71	.95	.84
belore	Dust Toss	٢	0	0	.00	0	.25	.25	I	1.0	1.0	.71	.67	.95	.84
	Head Rub	œ	0	0	.10	0	0	60 .	0	I	1.0	.70	.65	.91	.84
	Side Rub	6	0	0	.10	0	0	0	0	0	I	.67	.67	.90	.88
	Rise	10	0	0	.14	0	.13	.17	.29	.30	.33	I	.75	.95	.84
	Exit	11	0	.05	.23	.25	.29	.29	• 33	.35	.33	.25	I	. 68	1.0
	Ruffle-Shake	12	0	0	.05	.05	.05	.05	.05	60 .	.10	• 05	.32	I	.78
	Other	13	0	• 06	.12	.16	.16	.16	.16	.16	.12	.16	0	.22	ł

The average probabilities of first occurrences of components in relation to other components for test 3.

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			Ч	7	m	4	Ś	9	٢	80	6	10	11	12	13
	Enter	1	I	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
	Scratch	2	0	I	.50	1.0	1.0	1.0	1.0	1.0	1.0	1.0	•94	1.0	1.0
	Peck	e	0	.50	I	.93	.93	.93	•93	.93	.93	•93	.87	.93	.93
	Squat	4	0	0	.07	I	1.0	1.0	1.0	1.0	1.0	1.0	.94	1.0	1.0
	Peck	Ś	0	0	.07	0	I	.67	.67	1.0	1.0	1.0	.94	1.0	1.0
	Scratch	9	0	0	.07	0	.33	I	.61	.94	.94	•94	.88	.94	.94
Del Ore	Dust Toss	٢	0	0	.07	0	.33	.39	ı	1.0	1.0	.83	.88	1.0	• 6•
	Head Rub	œ	0	0	.07	0	0	• 06	0	I	1.0	.83	.88	1.0	• 64
	Side Rub	6	0	0	.07	0	0	• 06	0	0	1	.50	.72	.83	.75
	Rise	10	0	0	.07	0	0	• 06	.17	.17	.50	ı	•94	1.0	1.0
	Exit	11	0	• 06	.13	•06	• 06	.12	.12	.12	.28	• 06	I	.56	1.0
	Ruffle-Shake	12	0	0	.07	0	0	• 06	0	0	.17	0	44.	I	.81
	Other	13	0	0	.07	0	0	• 06	• 06	•06	.25	0	0	.19	1

probabilities (across all birds) associated with the first occurrence of a component preceding or following the first occurrence of any of the other components for all three tests. In general, these tables reveal that the ordering of the first occurrence of some of the components is highly structured. The most stereotyped aspect of the sequence involves the first occurrences of the dust toss, head rub and side rub components. In agreement with the observations of Borchelt, et al., (in press), at least one dust toss preceded the first head rub, and at least one head rub preceded the first side rub. Also the first occurrence of the ruffle-shake component was highly likely to occur only after the first dust toss had occurred. The ordering of the other components was, however, less stereotyped.

After the bird entered the dust, it was about equally likely for either the initial scratch or peck component to occur. The ordering of the other components was more variable, although patterns of probable occurrences are evident. The ordering of the scratch and peck while squatting components was most variable between tests, but neither these differences, nor any of the other differences between tests, were statistically significant (McNemar test for the significance of changes, Siegel, 1956).

Tables 3, 4 and 5 oversimplify the organization of the sequence of components by only considering the order of the first occurrence of each component. Many components occur successively and considerable recycling between components also occurs throughout the sequence for each bird. A conditional probability matrix constructed for each bird (or group) would adequately present the probabilities of occurrence

of com compor out th follow signif A duri ties w condit arity, an ent To tes were d to fir first quences dust to The cor Were co sequenc ^{test} 1 ^{occurre} second U-Tests ^{between} ^{for} thes of combinations of components, but only if the probabilities of various components exhibited stationarity; that is, remained constant throughout the sequence. For instance, if the probability of component B following component A during the beginning of the sequence is not significantly different than the probability of it following component A during the middle and end of the sequence, the conditional probabilities would exhibit stationarity or show a lack of time trends. If the conditional probabilities for all of the components exhibited stationarity, a conditional probability matrix for all of the components for an entire sequence would accurately reflect the ordering of components. To test for stationarity, the test 1 and test 2 sequences for each bird were divided into five subsequences (enter to first squat, first squat to first dust toss, first dust toss to first head rub, first head rub to first side rub, first side rub to end of sequence). These five subsequences correspond to the only components in the sequence (enter, squat, dust toss, head rub, side rub) whose order of occurrence was invariant. The conditional probabilities associated with the occurrence of components were computed for each of these subsequences. A comparison between subsequences of the conditional probabilities of some of the components on test 1 is presented in Table 6, which shows the median probability of occurrence (+ quartile deviation (Q)) of one component given that a second component has occurred. Significant differences (Mann-Whitney U-Tests, Siegel, 1956) occurred in the median conditional probabilities between some of the subsequences, clearly indicating a lack of stationarity for these conditional probabilities.

A co Peck-Peck (standing)	<pre>mparison, betwee deviati Enter to Squat Mdn(Q) 50 (24) </pre>	<pre>n subsequences, o on (Q)) associate Squat to Dust Toss Mdn(Q) z=4.79</pre>	<pre>f the median conditiona d with the occurrences Subsequence Dust Toss to Head Rub Mdn(Q) 0 (0) z=1.76</pre>	<pre>1 probabilities (t q of components. Head Rub to Side Rub Mdn(Q) 0 (0)</pre>	uartile Side Rub to End Mdn(Q) 0 (25)
Peck-Peck (squatting) PPONENTS		53.6 (28.4) z=3.83	72.7 (5.7) 	z=4.93	53.8 (16.8)
C Dust Toss- Head Rub				25 (16.7) z=2.52	8.3 (8.8)
Head Rub- Dust Toss				25.7 (4.5) 	1.9 (3.4)
H ead Rub - Head Rub				50 (12.7) z=2.71	34.4 (12.2)

Two alternatives are available to represent the complexity and variability of the sequence of all of the components. An average order of components (along with average conditional probabilities and some indication of variance) could be constructed for all subsequences over all birds tested at each deprivation level. Such an average dustbathing sequence would, however, be too complex to easily depict and would not give a very clear picture of the large number of ways in which the components can be ordered, even within the constraints imposed by the high degree of stereotypy shown by some orders of components. Instead, the actual sequences of components and conditional probabilities associated with transitions between components within each subsequence for five birds are presented in figures 4 through 9. These individual sequences were selected to display the variability within sequences seen when the order of each occurrence of all components is considered and contrast sharply with the high degree of stereotypy revealed by considering only the order of first occurrences of each component.

Figure 4.--The sequence of components and conditional probabilities associated with transitions between components (male #1, test 1).



Figure 5.--The sequence of components and conditional probabilities associated with transitions between components (female #1, test 1).



Figure 6.--The sequence of components and conditional probabilities associated with transitions between components (male #2, test 1).



Figure 7.--The sequence of components and conditional probabilities associated with transitions between components (female #8, test 2).



Figure 8.--The sequence of components and conditional probabilities associated with transitions between components (male #4, test 1).

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GENERAL DISCUSSION

In summary, the results showed that the frequencies of some of the components, and the sequence of first occurrences of the components, were highly reliable. The frequencies of some of the components, particularly the dust toss, head rub, and side rub components, were also highly intercorrelated, and the probable sequence of the first occurrences of components revealed a high degree of stereotypy for some components. Significant changes occurred in the frequencies of many of the components with deprivation of dust, and the head rub and side rub components exhibited sex X deprivation interactions, with the frequencies of components increasing more for males than females. Dividing the entire sequence of components into subsequences revealed that the conditional probabilities of some components did not exhibit stationarity. If the sequence of all occurrences of each component within subsequences was considered, rather than only the first occurrence of components, a high degree of variability in orders and conditional probabilities was revealed.

Does the fact that aspects of the sequence are reliable, some components are intercorrelated, and at one level of analysis the sequence of some components is highly sterotyped mean that the dustbathing sequence in Bobwhite quail is a Fixed Action Pattern (FAP)? The defining characteristic of a FAP (Hinde, 1970, pg. 20-21) is that "although it may consist of a quite complicated spatiotemporal pattern of muscular contractions, (it) cannot be split into successive

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responses which depend on qualitatively different external stimuli (Lorenz, 1935, 1937; Tinbergen, 1942)." Additional diagnostic properties of the FAP (Barlow, 1968) are that it has common causal factors different from those of other fixed action patterns; once released, the stimuli triggering the FAP no longer exercise control over it; and its components appear in a predictable sequence in time with the interrelation of the parts constant, even though the "intensity" or completeness of the components may vary.

At one level of analysis, some components of the dustbathing sequence do appear in a perfectly predictable temporal pattern; that is, at least one dust toss always preceeds the first head rub and at least one head rub always preceeds the first side rub. There is also evidence that the completeness of the sequence of these components varies with deprivation. At one day of deprivation (test 1) all (24) birds exhibited the dust toss component, 23 birds (96%) the head rub component, and 20 birds (83%) the side rub component. At five days of deprivation (test 3) all birds exhibited each of these components. At deprivation levels less than one day, it is probable that fewer birds would exhibit the complete sequence of these components. Of course, at the level of analysis of the first occurrence of all of the components, the sequence ceases to be perfectly predictable, and merely probable. At yet a further level, considering each occurrence of all of the components, it is not possible to accurately predict just which of the components will be the next to occur.

It may be difficult to maintain that the eliciting stimuli for dustbathing cease to exert control over the expression of the behavior once it has been released. If one considers the dust as the eliciting

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stimulus, evidence for it continuously modulating the dustbathing sequence may be found in the high intercorrelations between the pecking while squatting component and the dust toss, head rub, and side rub components. The pecking component presumably loosens, or perhaps even shapes, the dust so these components can occur. Of course, this refers to the dust modulating successive occurrences of these components in this manner; determining whether or not the dust modulates the form of any single instance of one of these components will require much finer analysis. If one accepts that lipids on the plumage elicit dustbathing, then successive occurrences of these components are again influenced by the eliciting stimulus, since a (hypothetical) increase in lipids with deprivation of dust elicits a greater frequency of components. The same uncertainty, however, exists concerning the effect of lipids on the form of a single occurrence of a component as exists for such on effect with dust.

Some components meet the requirement of the last diagnostic property of the FAP (Barlow, 1968) since the dust toss, head rub, and side rub components are high intercorrelated, suggesting common causal functions. Assuming the lipid regulation model to be valid, these three components are the only ones which actually serve to get dust into the plumage.

Whether or not the dustbathing sequence fits the formal definition of the FAP, that it cannot be split into successive responses which depend on qualitatively different external stimuli (Hinde, 1970) depends upon which components are considered. They may meet the requirement since non-particulate stimuli (Benson and Schein, 1965; personal observation) do not elicit these components and presumably neither do

substances on the feathers other than lipids from the uropygial gland, although this has not been systematically tested. Whether quantitative differences in the type of dust or chemical composition of lipids makes a difference in measures of these components awaits further research. The other components that occur during the sequence such as pecking and scratching <u>are</u> elicited by a number of qualitatively different stimuli, such as food or aggressive encounters.

Thus, it appears that the dust toss, head rub, and side rub components fit the formal definition of a FAP and meet many of the properties described by Barlow (1968). However, the suggestion by Marler and Hamilton (1966) and Barlow (1968) that the term "Fixed Action Pattern" be replaced with Modal Action Pattern (MAP) is supported by the results of this study. The "fixedness" of the pattern of dustbathing components depends entirely on which level of analysis is chosen. Of course, in the present study, only the frequencies and sequences of these components were measured. Further research, perhaps using films of the sequence and recording the form, duration, and other measures of the components, will yield additional information concerning the degree of variability around this modal action pattern.

The preceding analysis of the dustbathing components can be viewed from another framework, namely the subdivision of behavioral sequences into appetitive, consummatory, and post-consummatory components (Denny and Ratner, 1972). Appetitive components of behavioral sequences are movements associated with orientation to and selection of particular stimuli, and are relatively variable, both for an individual and between individuals of the same species. The consummatory components correspond to the fixed action pattern (Lorenz, 1950) and are more

sterot rub, a of the retest freque two of A compon compor exhibi instan while genera freque signif increa compor gests consum and su betwee compon diseng ment i 1 quency resear sterotyped than the appetitive components. Thus, the dust toss, head rub, and side rub components can be considered consummatory components of the dustbathing sequence; these components exhibited high testretest correlation coefficients and were highly intercorrelated, the frequencies increased with deprivation of dust, and the frequencies of two of the components showed sex X deprivation interactions.

Although the distinction between the appetitive and consummatory components is generally difficult to make (Denny and Ratner, 1970), the components other than the dust toss, head rub, and side rub components exhibited different features from these consummatory components. For instance, although one of the initial components of the sequence, peck while standing, had a high test-retest reliability coefficient, it was generally not highly intercorrelated with other components, and the frequencies of both the initial peck and scratch components showed nonsignificant decreases with deprivation of dust in contrast to the increase in frequencies of other components. This difference between components affected and those not affected by deprivation of dust suggests that the initial peck and scratch components are appetitive to the consummatory dust toss, head rub, and side rub components. The squat and subsequent peck and scratch components are intermediate components between appetitive and consummatory components, and the ruffle-shake component is presumably a post-consummatory component which serves to disengage the bird from the dustbathing sequence preparatory to engagement in other consummatory behaviors such as eating and drinking.

The finding that deprivation of dust led to increase in the frequency of most components of the sequence replicates and extends the research of Borchelt, et. al, (in press). Observations made during

the present study also indicated that there was an increase in lipid on the feathers when Bobwhite quail were deprived of dust for 5 days. These observations lend further support to the hypothesis that lipid on the plumage elicits dustbathing. The finding that there is a sex X deprivation interaction for the head and side rub components further supports this hypothesis. Kar (1947) reported that the secretion of the uropygial gland in domestic chickens was influenced by testosterone. This would suggest that if lipid from the uropygial elicits dustbathing, then there should be a sex difference in some measure of dustbathing, with males showing more dustbathing than females.

A direct test of the lipid regulation model is the purpose of the next study, which will quantify the observed increase in lipid on the plumage of Bobwhite quail deprived of dust.
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EXPERIMENT 2

Introduction

Experiment 1 replicated and extended the results of Borchelt, et al., (in press) by finding that the frequencies of many of the components of the dustbathing sequence increased with an increase in the level of deprivation of dust, and that the frequencies of the head and side rub components increased more for males than females. The purpose of the present study is to determine whether the mechanism for this deprivation effect is lipid substance from the uropygial gland by quantifying the observed change in lipid on the plumage with deprivation of dust.

Subjects and Procedure

Sixteen male and twenty-six female Bobwhite quail (<u>Colinus</u> <u>virginianus</u>) approximately six months of age were divided into 4 groups. Group 1 (4 0, 5 Ω) was deprived of dust for 1 day, group 2 (5 0, 6 Ω) for 5 days, group 3 (2 Ω , 7 Ω) for 15 days, and group 4 (5 0, 8 Ω) was deprived for 180 days (never allowed access to dust). Prior to the appropriate level of deprivation, groups 1, 2 and 3 were given 7 days continuous access to dust.

Groups 1, 2 and 3 were raised from chicks in the same laboratory as birds in experiment 1 and were housed in cages $137 \times 50 \times 30$ cm. on a 14:10 light-dark cycle. Groups 4 was maintained at the Department of Poultry Science Farm under continuous light in a 100 x 75 x 24 cm. cage with approximately fifty other birds until 5 months of age when

they were transferred to a cage identical to the cages of the other groups. Food (King Milling Company, Lowell, Michigan, U.S.A.) and water were continuously available at all times to each group.

After the appropriate period of deprivation of dust, all birds in each group were sacrificed (ether asphyxiation). The feathers of each bird were then cleaned with compressed air to remove any remaining dust from the plumage. The distal portion of most of the feathers (except the primaries) of each bird were clipped off with scissors, leaving the calamus intact. A 2-3 gm. sample of feathers from each bird was weighed and subjected to a standard ether extraction procedure on a Goldfisch apparatus for 2 hours. The collected lipid and ether were poured into tared containers, the ether evaporated, and the remaining lipid weighed on a Mettler analytical balance to an accuracy of 1 mg. Replicate samples of feathers were run from birds in groups 1, 2 and 4. No differences were found between replicates and the data are combined for each group.

Results

The results are shown in Figure 9 which depicts the mean amount $(\pm$ standard deviation) of lipid, expressed in mg. lipid per gm. feathers, for each of the groups. A one-way analysis of variance revealed the change in amount of feather lipid with deprivation of dust to be highly significant (F = 79.4, df = 3/38, p < .001). Comparisons between individual groups using the Newman-Keuls procedure (Winer, 1962) indicated that all of differences were highly significant (p < .001) except for the difference between groups 2 and 3, which was not significant. No difference was found in amount of lipid between male and female birds.

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Figure 9.--Mean amount (\pm standard deviation) of lipids on the feathers of birds deprived of dust for 1, 5, 15, or 180 days.



Discussion

The results clearly show that between 1 and 5 days of deprivation of dust there was a significant increase in feather lipid, confirming the observations of Borchelt, et al., (in press) and Experiment 1, and providing strong support for a lipid regulation model of dustbathing in Bobwhite quail.

The results of the present study have to be considered in view of reports that avian plumage contains lipid other than secretions from the uropygial gland. Bolliger and Varga (1960, 1961) and Bolliger and Gross (1958) have reported an average of approximately 2 percent total feather lipid (percent of dry feather weight) in a number of species of birds. These investigators suggest that the endogenous lipid is probably formed as a by-product of keratinization. The results of the present study, in which percent of total feather lipid ranged from 0.5 to 3.5, indicates that such endogenous feather lipid is certainly supplemented by lipid from the uropygial gland and the total amount of lipid can be regulated by dustbathing.

The lack of a significant increase in feather lipid between 5 and 15 days of deprivation suggests that there may be no increase in the frequency of dustbathing components between these two deprivation levels. This could occur if the frequency of "oiling" behavior levels off between 5 and 15 days of deprivation although the frequency of "oiling" does not reach an asymptote at 15 days since after 180 days of deprivation there was again a significant increase in feather lipid. It is also possible that this finding is due to a difference in conversion of dietary fats to lipid secretion from the uropygial gland

(Apandi and Edwards, 1964) since the weights of the birds in group 3 averaged about 20% less than in the other groups (160 gm. vrs. 200 gm.). Further research investigating both the changes in dustbathing behavior between 5 and 15 days of deprivation, and the relations between dietary fats, body weight, and feather lipid, will be necessary to resolve this discrepancy.

The lack of a sex difference in amount of feather lipid is surprising in view of the sex differences found in the head and side rub components in the previous study. The procedure in the present study for depriving the birds of dust, however, was different than in experiment 1. Since the birds in this study were housed in large groups and since groups of Bobwhite quail form dominance hierarchies, the birds were given one week of access to dust prior to deprivation to reduce the chance that birds low on the hierarchy would not have an opportunity to dustbathe. This is in contrast to the two days access to dust given in experiment 1. An alternative explanation for a lack of a sex difference is that feathers from the entire body surface of the birds were analyzed. It is possible that the smaller feathers of the head and flanks of the bird differed in amounts of lipid for males and females, but this difference was obscured by the larger percentage of feathers from the breast and back of each bird. Support for this view is found in data presented by Bolliger and Varga (1960) showing differences in the chemical composition of feather lipid between small and large feathers of an unspecified species of duck. Clearly, biochemical anlysis of the lipid from both the uropygial gland and plumage of one species of bird will be necessary to elucidate the relations between sex, uropygial and feather lipid and dustbathing.

These results also cast doubt on the generally accepted thesis that dustbathing serves primarily to remove ectoparasites. (Simmons, 1964; Goodwin, 1956; Stoddard, 1931). No ectoparasites were observed on the feathers of birds in this or in previous studies (Borchelt, et al., in press; Experiment 1). Since the principle food of ectoparasites is lipid substance from the feathers (Dubinin, cited in Kelso and Nice, 1963), dustbathing could perhaps secondarily remove ectoparasites by reducing their food supply, as well as by dessicating them or interfering with their respiration. It is clear that dustbathing occurs in Bobwhite quail which do not have ectoparasites and the lipid regulation model is offered to explain the function of dustbathing in Bobwhite quail, and perhaps other avian species as well.

EXPERIMENT 3

Introduction

The results of experiment 2 provide strong support for the lipid regulation model for the function of dustbathing in Bobwhite quail. The purpose of the present study is to further test the model by examining the effects on dustbathing following surgical removal of the main source of lipid on the plumage, the uropygial gland. Elder (1954) reviewed a number of studies which attempted to determine the function of the uropygial gland by surgically removing it. The general conclusion, supported by some of his own experiments on ducks, is that removal of the uropygial gland leads to gradual deterioration in the condition of the plumage (which is temporarily improved with molting) resulting in faster wetting of the feathers, scaling and peeling of the skin and bill, and a lower rate of growth for glandless as compared to normal birds, presumably due to a greater energy loss in glandless birds as a result of a less efficient insulating layer of feathers.

Thus, the lack of lipid from the uropygial gland adversely affects the condition of the plumage; the temporary improvement with molting would be due to a renewal of feathers containing endogenous feather lipid. No behavioral measures have been made on such operated birds other than Elder's (1954) note that there was no reduction in "oiling" behavior when the uropygial is removed. According to the lipid regulation model, however, removal of the uropygial gland should lead to a decrease in dustbathing behavior since there is a decrease in lipid applied to the feather.

Subjects:

Seven pairs of Bobwhite quail used in experiment 1 were used as subjects for this experiment. Three pairs were randomly assigned to the experimental (operated) group, and two pairs each were randomly assigned to an undisturbed control group and a sham-operated group.

Procedure:

The experimental birds were individually removed from their cages, placed in a holder, and a topical anesthetic (Cetacaine) was applied to the skin surrounding the uropygial gland. As much of the uropygial gland as possible was surgically removed, the skin sutured, and the birds given a week to recover from the operation. Post-mortem examination of these birds after the experiment revealed that there was no remaining lipid material from the uropygial gland. The birds in the sham-operated control group were treated identically, except the anesthetic was applied to a small area of skin on the back of the bird, a small cut was made and sutured, and the bird was returned to its cage. These birds were also given one week for recovery. The control birds were left undisturbed in their cages during this time.

The results of the second test at one day of deprivation (experiment 1) were used as the baseline data for all of the groups. One week after the appropriate operations were made, all of the birds were tested again at one day of deprivation with two days access to dust prior to deprivation. Two additional tests were given at weekly intervals for all groups. The recording procedures remained the same as in experiment 1 for all of the tests.

Results and Discussion

Each bird engaged in at least one dustbathing sequence on each of the three post-operative tests. Only the dust toss, head rub, and side rub components of the dustbathing sequence were analyzed since these are the only components directly involved in getting dust onto the birds' plumage. Figure 10 presents the results of the baseline test and the three post-operative tests for each of the three components. No statistical analyses were made on these results, since it is clear that there was no systematic decrease in the experimental group, and that the shamoperated group did not recover to baseline levels during any of the three post-operative tests.

The results of this study are disappointing in that they showed no systematic decrease in the frequency of either the dust toss, head rub, or side rub components in birds which had the uropygial gland removed. These birds, however, had extensive experience with dustbathing. It is possible that the lipid regulation model, as illustrated in Figure 1, may have to include an "experience" factor in the feedback loop between the uropygial gland and dustbathing (see Appendix). This possibility can be tested by removing the uropygial gland from different groups of birds either experienced or inexperienced with dustbathing. An additional factor may also be experience with "oiling"; this would necessitate removing the uropygial gland from different groups of birds either before or after experience with "oiling" ("oiling" is first seen at about 17 days of age in Bobwhite; Nitschke, 1972). This explanation of the results of the present study is quite plausible since other instances of interactions between experience and the behavioral effects of hormones occur in other classes of consummatory behaviors, for instance, sexual behavior (Rosenblatt



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A reasonable prediction from this explanation would be that increasing the deprivation level for the birds in this experiment would have resulted in no deprivation effect if they were dustbathing only due to extensive past experience rather than to remove lipid from the feathers. This also implies that there would have been no increase in lipid with deprivation of dust for these birds. Lipid could be experimentally applied to the birds' feathers to determine whether it could again elicit increases in dustbathing.

GENERAL DISCUSSION

The results of these three studies suggest some interesting areas for future research. First of all, dustbathing is a very robust behavior, with all birds engaging in a dustbathing sequence even at low levels of deprivation. Dustbathing is a good model for analysis of the structure of behavioral sequences since it contains a large number of components, some of which, at least in terms of first occurrences, are relatively stereotyped. Observation during these experiments also suggests that the durations of some of the dustbathing components are relatively constant. Of course, analysis of films of these components would be necessary to determine the average duration and degree of variability of components.

Benson (1965) filmed some of the dustbathing components of <u>Coturnix</u> quail at 200 frames per second and found that the duration of the dust tossing component averaged 1.12 seconds for one bird and 1.13 per another; unfortunately, no data on the variability of these durations are reported. Use of films would allow for a much finer analysis of individual differences as well as degree of stereotypy and variability. Such analyses are not only theoretically interesting for their information concerning either the validity of conventional definitions of fixed (or modal) action patterns, or for their use in analysis of appetitive, consummatory, and postconsummatory components of behavioral sequences, but they may also yield information helpful for making finer classifications of behavior. In addition, they may also serve as convenient baselines to assess the effects of variables on aspects of the behavioral sequence.

The second experiment provided compelling support for the lipid

regulation model, but future research could provide more direct evidence for the model by experimentally manipulating the level of lipid on the plumage. Several commercial products suitable for this purpose are available. A vegetable oil product (Pam) in aerosol cans could be sprayed in measured amounts onto the plumage, which should lead to an increase in dustbathing behavior. Several products are also available for removing lipid from human hair and would probably function the same for uropygial lipid. While these are highly artificial means of modifying the amount of lipid on the feathers of birds, positive results would greatly strengthen support for the lipid regulation model.

Suggestions can also be made concerning future areas of concentration for field studies of dustbathing and other COBS behaviors. If the lipid regulation model is valid, then differences in lipid production between male and female birds is expected. This suggests, of course, that differences should occur between males and females in dustbathing and perhaps other COBS behaviors. Seasonal differences should also occur, since photoperiods strongly affect production of reproductive hormones (Sturkie, 1965). Field studies to date have generally not reported data concerning sex differences in COBS behaviors because such differences have not been looked for.

The third study was less conclusive than the other two. Future research should consider the experience of the bird with both dustbathing and "oiling", and should assess the level of lipid on the feathers and record dustbathing behavior at different deprivation levels for birds with the uropygial gland removed. An alternative method for manipulating the amount of lipid from the uropygial gland is removal of the testes, which eliminates production of testesterone, which in turn should reduce the sex difference found in some measures of dustbathing.

In summary, these studies begin behavioral analysis, using the stages of the comparative method (Denny and Ratner, 1970), of a system or class of behaviors which have previously only been described. Guiding questions for future research should focus on determination of the mechanisms underlying the operation of this behavioral system with the goal of discovering whether the system functions on the same principles of operation as do other systems. Such analyses on these and other behavioral systems, on a variety of species, are necessary to attain a general, comparative psychology.

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APPENDIX

APPENDIX

The original formulation of the lipid regulation model is shown in Figure 11. This model assumes that both dustbathing and oiling behaviors are regulated by the bird to maintain within certain limits the amount of lipids on the plumage. Observations during both the Borchelt, Eyer and McHenry study and experiment 1 indicated that oiling behavior is not regulated since it does not decrease with deprivation of dust. These observations thus conflict with the original lipid regulation model. Eowever, by constructing a mathematical formulation of this model, it can be discovered that the graphic representation (Fig. 11) conflicts with the results of experiments 1, 2 and 3 as well. The first mathematical model presented in this section illustrates this point. In contrast, a second mathematical model was constructed to correspond to the lipid regulation model illustrated in Figure 1, which assumes that dustbathing is regulated while oiling is maintained at a constant rate. Some implications of this second model will be discussed.

Original Formulation

Model I was formulated as follows: Let: $F_N = Amount$ of lipids on feathers at time N $O_N = Amount$ of oiling behavior at time N $D_N = Amount$ of dustbathing at time N $\mu = Critical$ level for amount of lipids on feathers

Figure 11.--An fillustration of the original lipid regulation model.

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The following equations describe the relations between these variables:

 $F_{N+1} = F_N + \beta O_N - \alpha D_N \qquad (F_{N+1} \ge 0)$ $O_{N+1} = 0, \text{ if } F_N > \mu$ $\alpha(\mu - F_N), \text{ if } F_N < \mu$ $D_{N+1} = 0, \text{ if } F_N < \mu$ $\alpha(F_N - \mu), \text{ if } F_N > \mu$

Suppose the parameters for these equations are:

 $\alpha = 2$ $\alpha = \beta = 1$ $\mu = 5$.

This model yields the following time course with starting values of $F_N = 10$, $O_N = 0$, $D_N = 0$. The time units are given in days.

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Time	F _N	° _N	D _N
0	10	0	0
1	10	0	10
2	0	0	10
3	0	10	0
4	10	10	0
5	20	0	10

At this point, dust is removed and the birds given one day of deprivation of dust.

6 10 0 10

Now the birds are given access to dust.

Test 7 10 0 10

Using the same initial values prior to deprivation the birds in another experimental group are given five days of deprivation of dust and then access to dust.

	Time	F _N	0 _N	D _N
	0	20	0	10
	Five	10	0	0
	days	10	0	0
	of	10	0	0
	dust	10	0	0
	deprivation	10	0	0
Test	6	10	0	10

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As can be seen, the value of D_N is 10 units after both one and five days of deprivation, which conflicts with the results of the Borchelt, et al. study and experiment 1. It is also obvious that the value of F_N does not increase with deprivation of dust, which conflicts with the results of experiment 2.

This model predicts the following for experiment 3:

Time		F _N	0 _N	D _N
baseline <u>Test</u> 0		20	0	10
1	Remove	uropygial	gland	
one week of		10	0	0
recovery (de	epri-	10	0	0
Va	cion)	10	0	0
		•		•
		•		•
		•	•	•
Access to de	ust 8	10	0	10
Access to de	ust 9	0	0	10
	10	0	0	0
Post-operative Test-1	11	0	0	0

These values continue for all subsequent post-operative tests.

The data from experiment 3 do not correspond to the predictions of Model I. Model I predicts a decline in the value of D_N to zero on the first and subsequent post-operative tests.

Alternative Starting Values

Starting with different values will indicate the generality of the predictions of Model I. With initial values of $F_N = 0$, $0_N = 0$, $D_N = 10$, it can be seen what the model will predict in the case where the initial level of lipids on the feathers is below the critical level, μ .

	Time	^F N	0 _N	D _N		
	0	0	0	10		
	At this poin of deprivati	t dust is removed and on of dust.	the birds	given one day		
	1	0	10	0		
	Now the bird	s are given access to	dust.			
	2	10	10	0		
	In another group of birds.					
	0	0	0	10		
	Five	0	10	0		
	days	10	10	0		
	of	20	0	0		
	dust	20	0	0		
	deprivation	20	0	0		
Test	6	20	0	30		

If the initial value of F_N is below μ , then there will be an increase in both F_N and D_N with an increase in deprivation of dust. This increase will occur, however, at any time after three days of deprivation and the values of F_N and D_N will not continue to increase. Thus, with these starting values, Model I does not correspond to the results of the Borchelt, Eyer and McHenry study which found an increase in frequency of dustbathing from 1 to 3 days of dust deprivation, and a continued increase to 5 days of deprivation. Model I also does not predict, with these initial values, the results of experiment 2 which showed continued increases in the value of F_N . Unfortunately, Model I predicts an eventual leveling off of the values of F_N and D_N with time.

What about experiment 3?

	Time		F _N	0 _N	D _N				
ba seli ne Test	0		0	0	10				
1686		remove oil gland							
	one week of		0	0	0				
recovery (depri vation	ri-	0	0	0					
	n)	0	0	0					
			•	•	•				
			•	•	•				
			•	•	•				
	Access to dust	8	0	0	0				
	Access to dust	9	0	0	0				
	Deprivation	10	0	0	0				
Post-opera	tive Test-l	11	0	0	0				

These values continue for all subsequent post operative tests. With these new initial values, Model I still does not predict the results of experiment 3.

Alternative Formulation

From these considerations, as well as the observations that frequency of oiling behavior does not decrease with deprivation of dust, it is clear that a new model is called for. Model II incorporates a constant level of oiling behavior. A second constant sets a minimum level of D_N due to functions other than lipid regulation (such as removal of ectoparasites or because it "feels good").

The following equations describe Model II:

$$F_{N+1} = F_N + \beta O_N - \alpha D_N$$

$$O_{N+1} = K_1$$

$$D_{N+1} = K_2, \text{ if } F_N < \mu$$

$$\alpha(F_N - \mu), \text{ if } F_N > \mu, K_1 > K_2$$

Suppose the parameters stay the same as in Model I.

 $\alpha = 2$ $\alpha = \beta = 1$ $\mu = 5$ and $K_1 = 5$ $K_2 = 2$

The time courses of the values of F_N , O_N , and D_N can be computed for each of the three experiments as was done for Model I. The initial values are as follows: $F_N = 10$, $O_N = 4$, $D_N = 2$.

Time	F _N	0 _N	D _N
0	10	4	2
1	12	4	10
2	6	4	14
3	0	4	2
4	2	4	2
5	4	4	2
6	6	4	2

	one day depriv tion	a- 8	4	0	
Test	8	12	4	6	
	0	6	4	2	
	Five	8	4	0	
	days	12	4	0	
	of	16	4	0	
	dust	20	4	0	
	deprivation	24	4	0	
Test	6	28	4	38	
Thus, with	Model II, a dep	rivation eff	ect is obtained for a	D _N as found in	
experiment	l and there is	an increase	in F _N as found in ex	periment 2.	
	What about exp	eriment 3?			
	Time	F _N	0 _N	D _N	
b aseline <u>Test</u>	0	6	4	2	
	r	emove oil gl	and		
	one week of	8	0	0	
	recovery (depr vatio	1- 8 n)	0	0	
		•	•	•	
		•	•	•	
		•	•	•	
	Access to dust	8 8	0	6	
	Access to dust	92	0	6	
	Deprivation	10 0	0	0	
	Test	11 0	0	2	

These values continue for all subsequent post-operative tests.

The time course for values of D_N as predicted by Model II correspond fairly closely to the actual results of experiment 3. The Model predicts that the value of D_N declines to (or stays at) the level of K_2 .

Alternative Starting Values

To indicate the generality of Model II, different starting values of $F_N = 10$, $O_N = 4$ and $D_N = 6$ will be used.

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	Time	F _N	0 _N		D _N
	0	10	4		6
	one day of deprivation	8	4		0
Test	2	12	4		6
	0	10	4		6
	Five	8	4		0
	days	12	4		0
	of	16	4		0
	dust	20	4		0
	deprivation	24	4		0
Test	6	28	4		38
Thus, with	different starting	values, Model I	I still	predicts	the
results of	both experiments 1	and 2.			
	For experiment 3:				
	Time	F _N	0 _N		D _N
b aseline <u>Test</u>	0	10	4		6
	remov	ve oil gland			
	one level of	8	0		0
	recovery (depri- vation)	8	0		0

			8	0	0
			•	•	•
			•	•	•
			•	•	•
	Access to dust	8	8	0	6
	Access to dust	9	2	0	6
	Deprivation	10	0	0	2
<u> Test</u>		11	0	0	2

These values continue for all subsequent post-operative tests. With these starting values, Model II again corresponds closely to the results of experiment 3, since the value of D_N does not decline to zero, but to the value of K_2 . The degree of decrease in D_N from the baseline test 2 to post-operative test 1 will depend, however, on the initial level of D_N .

A comparison between the two models is shown in Tables 7 and 8. Table 7 shows which experiments can be predicted by Model I and II. Table 8 traces a time course of values of F_N , O_N , and D_N when the two models are allowed to continue for a period of time. As can be seen, the values predicted by each model exhibit cycles, with more extreme fluctuations in values exhibited by Model I than Model II.

Implications for Further Research

Table 7 shows that Model II predicts a less variable time course for values of D_N than does Model I. However, there is still change over time in the value of D_N , which suggests that the time span between reliability tests may be an important determinant of the reliability coefficient obtained for the frequency of dustbathing components. Model II also employs a constant (K₂) which sets a lower limit to the value of D_N . Experimental manipulation of K₂ (perhaps through modifying the

Table 7

A comparison of predictability of Models I and II.

Predicts results of	Model I	Model II					
Experiment 1	No	Yes					
Experiment 2	No	Yes					
Experiment 3	No	Yes					
			••				
------	----------------	----------------	----------------	----------------	----------------	----------------	--
	Model I			М	Model II		
Time	F _N	0 _N	D _N	F _N	0 _N	D _N	
0	10	4	2	10	4	2	
1	12	0	10	8	4	10	
2	2	0	14	2	4	6	
3	0	6	0	0	4	2	
4	6	10	0	2	4	2	
5	16	0	2	4	4	2	
6	14	0	22	6	4	2	
7	0	0	18	8	4	2	
8	0	10	0	10	4	6	
9	10	10	0	8	4	10	
10	20	0	10	2	4	6	
11	10	0	30	0	4	2	
12	0	0	10	2	4	2	
13	0	10	0	4	4	2	
14	10	10	0	6	4	2	
15	20	0	10	8	4	2	

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A time course of values of F_N , O_N , and D_N for Models I and II.

experience of the bird) would yield different time courses for D_N after removal of the uropygial gland. Moreover, since K_2 requires some minimum amount of dustbathing regardless of the level of F_N , a systematic decrease in D_N with removal of the uropygial gland would have been found in experiment 3 if very high levels of F_N were present at the start of the experiment. Thus, perhaps presenting a deprivation period of 5 days (rather than 1 day) prior to the post-operative tests would have led to more positive results. Also, the model is sensitive to slight changes in procedure. For instance, if only one day of access to dust were presented prior to the post-operative tests, the predicted results for experiment 3 would have been different.

