INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.

ProQuest Information and Learning 300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA 800-521-0600





MECHANISMS INFLUENCING ADOPTION IN THE COMMON TERN (STERNA HIRUNDO)

by

Margaret S. Friar

A Dissertation

Submitted to the University at Albany, State University of New York in Partial Fulfillment of

the Requirements for the Degree of

Doctor of Philosophy

College of Arts & Sciences

Department of Biological Sciences

2003

UMI Number: 3107598



UMI Microform 3107598

Copyright 2004 by ProQuest Information and Learning Company.
All rights reserved. This microform edition is protected against unauthorized copying under Title 17, United States Code.

ProQuest Information and Learning Company 300 North Zeeb Road P.O. Box 1346 Ann Arbor, MI 48106-1346 This page is intentionally blank.

ABSTRACT

I investigated mechanisms influencing adoption behavior in the common tern (*Sterna hirundo*). I defined adoption in the Laridae and treated the adoption process as two distinct steps: (1) wandering followed by (2) acceptance into a new nest. I conducted two series of field experiments and evaluated data from an eight-year observational study directed by Dr. Ian C. T. Nisbet. All investigations were conducted on Bird Island or Ram Island in Buzzards Bay, Massachusetts.

My analysis of the observational study data showed that chick wandering is neither rare nor widespread, occurring at a rate of 16% of all nests studied. Twenty-six percent (26%) of wandering chicks survived to fledge, compared to an overall survival rate of 44%, and stay-at-home siblings of wandering chicks realized the highest survival rate (57%). Most adoptions occurred at nests where the oldest chick was four-days or less old.

In the first of my two series of field experiments, I investigated fitness costs and benefits to both parents and chicks through brood manipulations.

Transferred chicks generally realized both direct and indirect fitness benefits because they and their stay-at-home siblings both had higher survival rates than control chicks of the same hatch rank. Parents of transferred chicks also gained fitness benefits, while parents at augmented broods suffered fitness losses due to lower survival rates of their own chicks.

In the second of my two series of field experiments, I investigated mechanisms involved in chick wandering by temporarily removing one member of a parent-pair. Removing one parent resulted in higher levels of aggression directed towards experimental broods and significantly higher wandering rates. These results suggest that wandering can be triggered by either deficiencies in parental care or aggression directed towards chicks.

My results support the view that both wandering chicks and their parents stand to realize fitness gains. If parents actively induce wandering, then adoption can be interpreted as a parasitic strategy facilitated by the timing of parent-offspring recognition.

PREFACE

The field experiments described in this dissertation were conducted under scientific collecting permits issued by the USF&WS (#MB778956-0) and the Massachusetts Division of Fisheries and Wildlife (155.98SCB, 136.99SCB, 094.00SCB, and 035.01SCB) and under University at Albany IACUC Protocols #98-010 and #00-003. The Medical Associates Recombinant DNA Lab at Loras College, Dubuque, IA, performed DNA sex determinations. My research was supported in part by financial grants from the University at Albany Graduate Student Organization and the SUNY Benevolent Association and through the generosity of Dr. Ian C. T. Nisbet.

My committee consisted of Dr. Kenneth P. Able, who was Chairman, Dr. Jerram L. Brown, Dr. Ian C. T Nisbet, and Dr. George R. Robinson. I am very grateful to each of them for their guidance and encouragement.

I value the interest and encouragement of Dr. Ingrid Peters, Esther Brown, and Alice Jacklet, all of whom visited my research site for first-hand exposure to an active tern colony. Alice also provided useful comments on my manuscript and valuable insight and experience while I was her teaching assistant. Dr. Tram Neil provided useful suggestions on data analysis. Dr. Jeremy Hatch provided insight and encouragement during a total of six field seasons at Bird Island. Dr. Steve Brown and Dr. Jeff Travis have each been mentor, role model, supporter, and friend. I am grateful for the assistance of Ann Boehm and Blanche Feck in the Biology Department Office.

Suzanne Conlon assisted me with my fieldwork in 1999 and Courtney Redmond assisted me during 2000 and 2001. Without their help, I would have been unable to accumulate the volume of data in the experiments. I am grateful to Dr. Jennifer Arnold, a fellow Bird Island researcher, for her assistance and encouragement. I am grateful to the various managers and field assistants working on the Buzzards Bay Tern Project for their help and companionship during my fieldwork. I am enormously grateful to Dr. Ian C. T. Nisbet. In addition to serving on my committee and providing financial support and data from his own adoption studies, he has been both the inspiration for my research and a rare and valued mentor during a total of six field seasons and the ensuing years.

I am grateful to my parents for their support and to my husband, Glenn Friar for his unwavering support, assistance, and encouragement.

TABLE OF CONTENTS

	Page
ABSTRACT	iii
PREFACE	V
LIST OF TABLES	x
LIST OF ILLUSTRATIONS	xvi
Chapter	
I. ADOPTION BEHAVIOR IN THE <i>LARIDAE</i>	
Introduction Terminology Explanation for Adoption in the Laridae Hypotheses and Predictions Recognition Error / Maladaptation Kin Selection Reciprocal Altruism Intergenerational Conflict Summary of Hypotheses and Predictions Research Objectives Operational Definition of Adoption Theoretical Framework for Analyses Objectives of my Research	4 5 7
II. GENERAL METHODS	
Distribution and Habitat of the Common Tern Study Sites Ram Island Bird Island	
Field Protocols Nests and Eggs Chicks Adults	30
Descriptive Equations and Statistical Methods Chick Growth Characterization Costs and Benefits Data Recording and Statistical Analyses	33

III. BIRD ISLAND ADOPTION STUDIES, 1987-94

	IntroductionSummary of Methods and Conventions Employed by the	38
	Investigators Description of Information Collected by Observers	
	Methods Wanderings, Adoptions, and Fledging Costs and Benefits Data Organization	43
	Results Data Reduction Data Evaluation	47
	Discussion and Conclusions Observations on the Data Derived from the Bird Island Adoption Studies Relation to Brood and Parental Manipulation Experiments	73
IV.	COSTS AND BENEFITS OF ADOPTION: BROOD MANIPULATION EXPERIMENTS	
	Introduction Hypotheses and Predictions Methods Nest Selection Egg Selection Transfer and Weighing Protocols	79 82 89
	Statistical Methods Results Growth Fledging Success Chicks Fledged per Nest, Filial Offspring Fledged per Pair, and Hatching Intervals Costs and Benefits Summary of Statistically Significant Results	97
V.	Discussion and Conclusions MECHANISMS INFLUENCING CHICK WANDERING: PARENTAL CARE MANIPULATION EXPERIMENTS	133
	Introduction Hypotheses and Predictions Methods Preparations Experimental Protocols Statistical Methods and Definitions of Variables	

V. MECHANISMS INFLUENCING CHICK WANDERING: PARENTAL CARE MANIPULATION EXPERIMENTS (continued)

Results	156
Wanderings	
Parental Behaviors	
Aggressive Behaviors	
Chick Growth	
Sex Differences in Parental Care	
Summary of Results	
Discussion and Conclusions	178
VI. MECHANISMS INFLUENCING ADOPTION	
IN THE COMMON TERN	183
AFFEDENOSO	404
REFERENCES	194
APPENDIX: DATA FROM THE 1987-94 BIRD ISLAND ADOPTION	
STUDIES	200

LIST OF TABLES

Table		Page
l.	Categories of chicks for which information was collected in adoption studies on Bird Island during the 1987 through 1994 breeding seasons.	42
II.	Total number of chicks for which information was collected, shown by category and year in adoption studies on Bird Island during the 1987 through 1994 breeding seasons.	44
111.	Total number of chicks identified as having hatched regardless of post-hatching behavior in adoption studies on Bird Island during the 1987 through 1994 breeding seasons, shown by hatch rank when known.	48
IV.	Hatch rank of chicks identified as having wandered in adoption studies on Bird Island during the 1987 through 1994 breeding seasons.	50
V.	Nest rank at time of wandering of chicks identified as having wandered in adoption studies on Bird Island during the 1987 through 1994 breeding seasons.	51
VI.	Age at time of wandering by hatch rank of chicks identified as having wandered in adoption studies on Bird Island during the 1987 through 1994 breeding seasons.	52
VII.	Nest rank assumed at adoption by chicks identified as having been adopted in adoption studies on Bird Island during the 1987 through 1994 breeding seasons.	53
VIII.	Age of native A-chick in adopting brood on day of adoption for chicks that were identified as having been adopted in adoption studies on Bird Island during the 1987 through 1994 breeding seasons.	54
IX.	Total number of chicks of known hatch rank compared with those of them that were observed to wander in adoption studies on Bird Island during the 1989 through 1992 breeding seasons.	e 57

Table		Page
X.	Total number of chicks that were observed to wander compared with those that were observed to wander and then be adopted in adoption studies on Bird Island during the 1987 through 1994 breeding seasons.	58
XI.	Chicks that were observed to both wander and be adopted compared with chicks that were observed to wander, be adopted, and fledge in adoption studies on Bird Island during the 1987 through 1994 breeding seasons.	59
XII.	Total number of chicks that were observed to have hatched compared with chicks that were observed to have hatched, wandered, be adopted, and then fledge in adoption studies on Bird Island during the 1987 through 1994 breeding seasons	60
XIII.	Fledging outcome for chicks in nests that sustained neither wanderings nor adoptions ("Control Nests") recorded in adoption studies on Bird Island during the 1989 through 1994 breeding seasons.	61
XIV.	Fledging outcome for chicks for which rank, hatching, and fledging status were all recorded in adoption studies on Bird Island during the 1989 through 1994 breeding seasons.	62
XV.	Number of wandering chicks with known fledging outcome that were observed in adoption studies on Bird Island during the 1987 through 1994 breeding seasons.	63
XVI.	Number of siblings of wandering chicks that did not themselves wander from their natal nest and were observed to have hatched, compared with those observed to have both hatched and fledged in adoption studies on Bird Island during the 1987 through 1994 breeding seasons.	64
XVII.	Number of chicks that were nest mates of adopted chicks that had not themselves wandered from their natal nest and were observed to have hatched compared with those that were observed to have hatched and fledged in adoption studies on Bird Island during the 1987 through 1994 breeding seasons	65

Table	·	Page
XVIII.	Number of non-wandering siblings or nest mates that hatched in Donor-Adopter or Adopter-Donor Nests compared with those which were observed to have both hatched and fledged in adoption studies on Bird Island during the 1987 through 1994 breeding seasons.	. 66
XIX-a.	Number of filial offspring by nest type and hatch rank in nests fo which hatching and fledging were both observed in adoption studies on Bird Island during the 1987 through 1994 breeding seasons.	r 68
XIX-b.	Number of filial offspring by nest type, combining Donor with Donor/Adopter and Adopter with Adopter/Donor types, and hatch rank for nests in which hatching and fledging were both observed in adoption studies on Bird Island during the 1987 through 1994 breeding seasons.	. 69
XX.	Benefit (cost) as the comparison between filial offspring fledged per adult pair for Control and for Donor or Adopter categories of broods in Bird Island adoption studies during the 1989 through 1992 breeding seasons	. 70
XXI.	Quadratic Growth Rate (a _q) for A- and B-chicks in 1998 experiments by Brood Type and Nest Rank.	. 98
XXII-a.	Linear Growth Rate (a _I) for A- and B-chicks in 1998 experiments by Brood Type and Nest Rank.	. 100
XXII-b.	Linear Growth Rate (a _i) for all chicks in 1999 experiments by brood size, Brood Type, and Nest Rank.	. 101
XXIII.	Asymptotic Mass (AM) for chicks that fledged in 1998 experiments by Brood Type and Nest Rank.	. 103
XXIV.	ANCOVA comparing Asymptotic Mass (AM) by Brood Type with Laying Date by Nest Rank for chicks fledged from 3-chick broods in 1999 experiments.	
XXV.	Asymptotic Mass (AM) for chicks that fledged in 1999 experiments by brood size, Brood Type, and Nest Rank	. 105

Table		Page
XXVI.	Proportion of chicks that fledged by Brood Type, final brood size, year, Hatch Rank, and Nest Rank in 1998 and 1999 brood manipulation experiments.	106
XXVII-a.	Proportion of chicks that fledged of all chicks in 1998 experiments by Brood Type and Nest Rank.	108
XXVII-b.	Proportion of chicks that fledged of all chicks in 1999 experiments by brood size, Brood Type, and Nest Rank	109
XXVIII-a.	Proportion of chicks that fledged in 1998 experiments and Asymptotic Mass (AM) by Brood Type, Nest Rank, Hatch Rank, and nest replacement strategy.	114
XXVIII-b.	Proportion of chicks that fledged from 2-chick broods in 1999 experiments and Asymptotic Mass (AM) by Brood Type, Nest Rank, Hatch Rank, and nest replacement strategy	115
XXVIII-c.	Proportion of chicks that fledged from 3-chick broods in 1999 experiments and Asymptotic Mass (AM) by Brood Type, Nest Rank, Hatch Rank, and nest replacement strategy.	116
XXIX-a.	Fledging outcomes in 1998 experiments by Brood Type and nest replacement strategy as nest totals per adult-pair, with corresponding hatching interval.	121
XXIX-b.	Fledging outcomes for 2-chick broods in 1999 experiments by Brood Type and nest replacement strategy as nest totals per adult-pair, with corresponding hatching interval.	124
XXIX-c.	Fledging outcomes for 3-chick broods in 1999 experiments by Brood Type and nest replacement strategy as nest totals per adult-pair, with corresponding hatching interval.	125
XXX.	Results of 1998 and 1999 brood manipulation experiments showing benefit (cost) as filial offspring fledged for experimental broods compared to Control Broods.	. 126

Table		Page
XXXI.	Consequences of being a chick from a Reduced Brood or an Augmented Brood compared to a chick from a Control Brood in 1998 and1999 brood manipulation experiments, measured in terms of Fledging Success compared to Control Nest chicks of like Hatch Rank and natal brood size.	
XXXII.	Relative combined direct and indirect fitness benefit (cost) for a chick introduced into an Augmented Brood in 1998 and 1999 brood manipulation experiments, measured in terms of Fledging Success compared to Control Brood chicks of like Hatch Rank and natal brood size.	131
XXXIII.	Comparison of elements of combined direct and indirect fitness benefit (cost) for a chick introduced into an Augmented Brood from a Reduced Brood in 1998 and 1999 brood manipulation experiments.	. 131
XXXIV.	Summary of statistically significant relationships identified for chicks and Brood Types in 1998 and 1999 brood manipulation experiments.	. 132
XXXV.	Number of nests by year, nest type, and sex of adult removed from experimental nest in 2000 and 2001 parental care manipulation experiments.	. 148
XXXVI.	Nests with and without wandering chick(s) by year and nest type in 2000 and 2001 parental care manipulation experiments.	. 157
XXXVII.	Chicks that wandered (wanderers) compared with all chicks by age at wandering, nest type, and hatch rank in 2000 and 2001 parental care manipulation experiments.	. 159
XXXVIII.	Parental behaviors (attendance, brooding, and feeding) by nest type as fractions of watch duration in 2000 and 2001 parental care manipulation experiments.	. 160
XXXIX.	Parental behaviors (attendance, brooding, feeding, aggression, and nest defense) by the adult at experimental nests as fractions of watch duration in 2000 and 2001 parental care manipulation experiments.	. 162

Table		Page
XL.	Aggressive behaviors by nest type as fractions of watch duration (number/hour) in 2000 and 2001 parental care manipulation experiments.	164
XLI.	Chick growth as weight change after one and two days shown by chick age on the day of the experiment, chick rank, and nest type in 2000 and 2001 parental care manipulation experiments.	t 172
XLII.	Parental behaviors (attendance, brooding, feeding, overall aggression, and nest defense) by individual adults as fractions of watch duration in 2000 and 2001 parental care manipulation experiments.	175

LIST OF ILLUSTRATIONS

Figure	Э	Page
1.	Paths and Outcomes for a Chick After Hatching	19
2.	Buzzards Bay, MA and Surrounding Areas	25
3.	Ram Island, MA – 2000 Study Area	26
4.	Bird Island, MA – 1998 - 2001 Study Areas	28
5.	History of Common Tern Nesting Population, Fledging, and Adoptions on Bird Island, MA from 1970 through 1989	29
6.	Chick Growth Characterization	34
7.	1987-1994 Adoption Studies: Numbers of Chicks of Known Hatch Rank by Rank and Unknown Hatch Rank by Year	49
8.	1987-1994 Adoption Studies: Number of Wandering Chicks by Hatch Rank	50
9.	1987-1994 Adoption Studies: Nest Rank at Wandering	51
10.	1987-1994 Adoption Studies: Chick Age at Wandering	52
11.	1987-1994 Adoption Studies: Nest Rank at Adoption	53
12.	1987-1994 Adoption Studies: Age of the Native A-chick in an Adopting Brood on the Day of an Adoption	55
13.	1987-1994 Adoption Studies: Filial Offspring Fledged per Nest-pair for Adopter Broods and for Donor Broods Compared to Control Broods	71
14.	1987-1994 Adoption Studies: Filial Offspring Fledged per Parent-pair by Nest Type, Mean + 1 Standard Error	72
15.	1998 Replacement Strategy: A-chick to A- or B-position	86
16.	1999 Replacement Strategy: A- or B-chick to A-position in either a 2- or 3-chick Brood	88
17.	Linear Growth Rate (LGR) by Year, Natal Brood Size, and Nest Rank, Mean + 1 SD	99

LIST OF ILLUSTRATIONS (continued)

Figure		Page
18.	Asymptotic Mass for Fledged Chicks by Brood Type and Nest Rank, Mean +1 SD	102
19.	Proportion of Chicks that Fledged by Year, Brood Size and Type, and Nest Rank, Mean +1 SD	107
20.	Proportion of Chicks that Fledged and Asymptotic Mass, Mean ±1 SD, by Originating Brood Type, and Hatch and Nest Ranks	. 113
21.	Offspring Fledged per Pair for 1998 and 1999 Broods by Brood Type and Replacement Strategy, Mean +1 SD	118
22.	A-B and B-C Hatch Intervals for 1998 and 1999 3-chick Broods by Brood Type and Replacement Strategy, Mean +1 SD	119
23.	Parental Behaviors: Attendance, Brooding, and Feeding Rates for Experimental and Control Broods, Mean ± 1 Standard Error	161
24.	Overall Aggression Rate in Experimental and Control Broods with Box Plots showing Median, 75 th and 90 th Percentiles, and Outliers	166
25.	Nest Defense Rate in Experimental and Control Broods with Box Plots showing Median, 75 th and 90 th Percentiles, and Outliers	168
26.	Aggression Towards Brood Rate in Experimental and Control Broods with Box Plots showing Median, 75 th and 90 th Percentiles, and Outliers	170
27.	Chick Growth as Percent Weight Change between Day of Experiment and Day Following Experiment for Chicks Grouped by Age on Day of Experiment, Mean <u>+</u> 1 Standard Error	173
28.	Sex-biased Roles and Compensation by Single Birds, Mean + 1 Standard Error	176

CHAPTER I

ADOPTION BEHAVIOR IN THE LARIDAE

Introduction

Adoption and other forms of alloparental care, in which individuals other than the genetic parents provide care for young, have been documented in over 150 mammalian and 120 avian species (Riedman 1982). Many of the species involved in these cases share similar behavioral or social reproductive characteristics.

Alloparental care behaviors include "babysitting" and "helping", where young receive care from non-parents as well as parents. Adoption, on the other hand, is a form of alloparental care involving the fostering of another individual's young (Riedman 1982). In adoption, only foster parent(s), and not biological parents, care for young. Forms of adoption include "step parenting", where a replacement parent cares for the offspring of its mate (Plissner and Gowaty 1988); adoption by failed breeders (Jouventin et al. 1995); taking over of an entire brood (Larsson et al. 1995; Williams 1994); and assuming full care for a single (or a few) foreign young by breeders that are also caring for their own young (Brown et al. 1995; Bukacinski et al. 2000; Carter and Spear 1986; Gaston

et al. 1995; Graves and Whiten 1980; Holley 1981; Morris et al. 1991; Oro and Genovart 1999; Roberts and Hatch 1994; Saino et al. 1994). The last of these forms of adoption is the focus of this dissertation.

Among birds, differing patterns of adoption require distinct adaptive explanations. Altricial and semi-altricial species show lower rates of adoption than semi-precocial or precocial species (Oro and Genovart 1999). In precocial birds whose chicks feed themselves, costs to adopters seem to be minimal (Williams 1994; but see Codenotti and Alvarez 1998). Semi-precocial young, however, require brooding and feeding, so adoption in this case should involve a fitness cost to foster parents.

The remainder of this dissertation addresses the Laridae (gulls and terns), a family of seabirds with semi-precocial young. Their chicks are mobile almost from hatching, yet require extensive bi-parental care for thermoregulation and feeding (Hamer et al. 2002). Species in this family have life history characteristics that could lead to the evolution of cooperative reproductive traits such as adoption (Brown 1998). The adults are long-lived (Weimerskirch 2002) and show strong natal philopatry and nest site fidelity (Bried and Jouventin 2002). Colonial breeding is also common in gulls and terns. The close proximity of pairs nesting in open habitats with few physical barriers allows chicks to move among nests, providing the opportunity to solicit care and feeding from birds other than their biological parents. Adoption studies of members of this group are particularly interesting because, while adoption behavior can reduce the fitness of foster parents (Carter and Spear 1986; Graves and Whiten 1980;

Holley 1981; Riedman 1982), it is not rare. Adoption has been detailed in numerous gull and tern species.

I have chosen as my model for investigation, the common tern (*Sterna hirundo*), a highly social, ground-nesting, colonially breeding seabird with semi-precocial young. Common tern chicks hatch covered with down, yet require brooding during the first few days of life (Nisbet 2002). Modal clutch size is 3 eggs (Nisbet 2002). Siblings hatch asynchronously (Morris et al. 1991; Nisbet and Cohen 1975) over a period of 2.5 to 3 days or longer as the breeding season progresses (Nisbet and Cohen 1975). Chick survival declines with hatching order (Bollinger 1994), and adults fledge an average of between 1 and 2 chicks per year depending on environmental conditions (Nisbet 2002). Common tern chicks have been observed to wander from their natal nest and solicit care at other nests, usually within two days after hatching (Nisbet pers.comm.).

In general, wandering from the nest is risky for chicks, many of which die before they find a pair that will accept them. Except for the short period before adults learn to recognize their own chicks, most gulls and terns vigorously attack foreign young that enter their territories. This has been interpreted as a defense against the risk of adopting unrelated offspring (Ashmole 1963). Acceptance of a foreign chick is a rare failure of this defense mechanism.

Food is a limiting factor for terns because parents must leave the colony to forage for a single food item which is then carried back to the chicks (Fasola and Saino 1995; Nisbet 2002). Chick provisioning is generally more costly for terns

than for gulls because terns carry food in the bill and each food item requires a separate trip, whereas gulls are able to gather several prey items and then regurgitate to feed the chicks without the risk of losing food items to kleptoparasites. Thus, for terns, accepting a foreign chick into a brood should come at an even greater cost than it does for gulls because of the extensive parental care required to raise each chick.

Terminology

Alloparenting and adoption in mammals and birds have been the subjects of many studies. The related terminology has been used in slightly different ways throughout the literature. Here, I define some of the terms as I use them in the context of my study. "Adoption" is the exclusive fostering of another individual's offspring by parents that are also caring for their own young. "Wandering" is the departure of a chick from its natal or adoptive brood. Operational definitions for wandering and adoption are provided later in this chapter. Broods from which a chick has departed are called "donor broods" and broods in which an adoption has occurred are called "adopter broods". Parents of these broods are called "donor parents" and "adopter parents", respectively. I use the term "foreign" to refer to non-natal chicks and also distinguish them from adopted chicks (adoptees). I use the term "siblings" to describe biological siblings together or in separate broods and "nest mates" to describe chicks in a brood that are not biological siblings, e.g., an adoptee is a nest mate to chicks