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SUBJECT W caps

Feeding Behavior and Estimated Energy Budget of the Forster's Tern

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Well Done
Well Written
Well Analyzed

Abstract: Foraging behavior and success of the Forster's tern (Sterna forsteri) ^{was} studied at Tulelake National Wildlife Refuge, California.

Three methods of feeding were observed, contact dipping and hawking for insects, and surface plunging for fish. Feeding activity was bimodal with peaks between 0700-0900 and 1700-1900. Success rates and frequencies of hawking were highest (100%, 660 attempts/hour) followed by contact dipping (83%, 354 attempts/hour) and plunging (32%, 20/hour). Success rate and frequency of contact dipping were greatest at mid-day. Estimated cost for daily energy expenditure was 184.8^+ kcal/day. Daily caloric intake was estimated at 208.85 kcal/day ^{with most energy benefit derived from _____}. Activity was initiated at 64 lux and terminated at 67 lux. Foraging of dipping and plunging birds was directed against the wind. Intra- and inter-specific aggressive encounters were seen most often during fishing activity and appeared to detract from rate of plunging. Foraging behavior of juveniles observed was markedly different from that of adults.

Forster's terns (Sterna forsteri) forage by flying over open water. Salt and Willard (1971) investigated their hunting behavior and success rates over the span of one year. However, they studied only diving or "plunging" activity. Ashmole and Ashmole (1967) and Ashmole (1971) described several methods of feeding utilized by seabirds. Two of these: "surface

plunging" and "contact dipping"; are used by Forster's tern. Begg (1973) described another method, "hawking", also discussed by Bent (1921) and Pearson (1968). Terns use these methods to capture different prey types yielding highly varying caloric returns. Success rates and frequencies of these methods vary with the nature of the prey. In addition, the distribution and activity of a predator are largely determined by the distribution and activity of the prey (Orians, 1971; Schoener, 1971). Weather conditions can also affect the distribution and vulnerability of the prey species.

Specific information on foraging behavior of the Forster's tern is limited. The major objectives of this study were : (1) to describe the feeding behavior of Forster's tern and ; (2) to estimate the caloric costs and benefits of their foraging methods.

This study was conducted as part of the requirement for a B. S. degree in Wildlife and Fisheries Biology at the University of California at Davis. Many individuals contributed to this investigation. I acknowledge the Tulelake National Wildlife Refuge Staff for their cooperation, L. Candry for the use of his land as an observation site, B. W. Smith for his assistance in collecting data, H. W. Williams and T. J. Dormody for help in preparing and reviewing the manuscript, R. J. Boekelheide for his valuable comments and support, and several members of the Division of Wildlife and Fisheries Biology at the University of California at Davis. Special acknowledgement goes to Dr. D. G. Raveling and Dr. R. G. Schwab of the University of California, Davis, for their instruction and criticisms.

STUDY AREA

The study area was Tulelake National Wildlife Refuge and Lower Klamath National Wildlife Refuge in Siskiyou County, California. The main observation area was the 74,500 m² Sump 1-A on Tulelake Refuge (Fig. 1). Depths

of the sump ~~run~~ ^{vary} from <1 m to several meters along the dikes. The drainage ditches and channel between the sumps are deeper than the areas by the pump-houses and the ^{remainder} rest of the sump.

A large portion of the sump is covered with algae (Cladophora) mats. The roosting area in the main unit along Dike A (Area D) was composed of clumps of bulrush (Scirpus spp.). Cattail (Typha latifolia) surrounds^{ed} the border of the sump.

On 3 occasions I conducted observations in Lower Klamath National Wildlife Refuge (Fig. 2), in similar habitat.

METHODS

Daily observations were conducted from 26 June-14 July at different times for a total of 91 hours. Observations were conducted from various points on a dike encircling the sump with a pair of 8x30 binoculars and a 15x-60x zoom spotting scope. The spotting scope was used to observe birds feeding on the algae mat, 100-200 m offshore.

Numbers of birds involved in contact dipping, plunging to surface, sitting and, on one occasion, hawking, were recorded periodically. Height of terns over the water and their direction of foraging were noted.

Temperature, cloud cover, and wind conditions were recorded daily. Light meter readings were made with a Gossen Luna-pro light meter at 50 ASA with incident light for an hour around sunrise and an hour after sunset at approximately 10 minute intervals. Readings were taken with the meter pointed to the west, south and straight up, and averaged to determine lux at a particular time.

Prey capture efficiency of terns hunting on the algae mats was recorded by observing individual birds for approximately 4 minute periods with the spotting scope on 20x-25x. Success was judged by the bill motion of

the tern. If an insect was captured, the mandibles moved in a vertical "chewing" motion. On the 5 occasions I was close enough to see the prey taken, this motion always followed a capture and was not observed if the bird was not successful. Often a tern flew out of effective range within 4 minutes; when this occurred observation periods were terminated.

Efficiency of surface plunging birds was judged by visual sighting of prey taken during the period a tern was under observation. One individual was observed as long as possible. Terns usually swallow their prey in the air, so determination of success is possible (Salt and Willard, 1971). Plunges initiated but not completed were judged as no success during the last week of the study.

Efficiency and frequency of hawking activity was judged by timing them with a stopwatch for approximately one minute intervals and counting the captures, observed with binoculars. The distance from my observation point to the birds was 3-40 m, with the terns at a height of 1-10 m above the water.

Four birds could be identified as individuals due to plumage aberrations. Two of them were specifically observed at the pumphouses in Areas C and D.

Data were grouped ^{into} 2-hour blocks encompassing 16 hours from 0500-2100. The following mean values were calculated: observation time in minutes; numbers of plunges; number of dips; frequency, in attempts/hour; numbers of birds per time period; and efficiency. To evaluate differences at particular times of the day, data were grouped into 3 blocks (0700-1000, 1200-1500, and 1700-2000).

Insects on the algae mat were collected on 6 July with a sweep net from a canoe and others were identified visually. Specimens were weighed, identified to family and their caloric content determined from Cummins and Wuychek (1971).

Using bill lengths as an estimate of prey size, bill length being 5 cm (Salt and Willard, 1971), mean sizes of 25 captured fish were 3.0 ± 1.4 cm (S. D.). The average weight Tui chub (Gila bicolor) and blue chub (Gila operulea) of this length is 3 grams fresh weight, as determined by weighing frozen specimens previously collected by fisheries students at the University of California, Davis.

RESULTS

Description of Foraging Methods

Three basic foraging patterns were observed. Terns fed most frequently by contact dipping. Birds foraging in this manner flew low over the ^{algae mat} from < 1 m to 2 m above the surface, with the beak pointed downward almost continually. When prey was sighted, birds dipped down to pick the insect off the algae mat. Typically, only their bills entered the water. The terns then immediately returned to their original flying height except where prey appeared dense. In these circumstances, birds stayed 40-60 cm over the surface and dipped with a high frequency. Terns often dangled their feet while dipping and occasionally pushed off the water surface after a capture. With one exception, flight was uninterrupted and terns rarely alighted on the surface.

Contact dipping predominately occurred on the algae mats along Areas A, B, and D ^{(see Fig. 1).} On several occasions birds dipped over open water in the same areas.

Plunge-to-surface (Ashmole and Ashmole, 1967; Ashmole, 1971) was the major feeding method observed. Using this method, birds flew at a height of 6-10⁺ m over the water in a roughly circular pattern with the bill pointed downward. They periodically lifted their heads, apparently to keep themselves oriented. When prey was sighted, terns hovered with their wings held backward. Their wings were then folded and the terns "fell" headfirst into

the water, either partially or completely submerging. Terns usually capture prey within 30 cm of the surface (Salt and Willard, 1971). They did not pursue prey underwater. Often the body of the tern would twist as it entered the water, possibly following the prey's attempt to escape.

Fish caught ranged from 1.2 cm to 5 cm in length with an estimated average weight of 3 grams. If the prey item was large (>4-5 cm), birds performed an elaborate handling process--tossing the fish into the air, swooping down, and catching it. Terns repeated this several times, until the fish was eaten or dropped. I observed loss of prey 2 out of 6 occasions this behavior was observed.

Two pumphouses, one in the middle of Area D and one at the southwest corner of the sump, Area C, and a channel between the sumps, appeared to be the primary fishing areas. Terns also used irrigation ditches around the sump for fishing. The birds fished over open water, particularly when pelicans foraged. Usually 10⁺ terns fished at one time over a mixed group of white pelicans (Pelecanus erythrorhynchos), double-crested cormorants (Phalacrocorax auritus), and western grebes (Aechmophorus occidentalis): Observation times of one individual ranged from 5 minutes over open water up to an hour by the pumphouses.

I observed terns hawking, or capturing insects on the wing, only once, on 7 July, from 0900-1700 with a lull from 1300-1500, in Area A. Birds feeding in this manner flew from <1 m to 16 m above the surface of the water with their beaks pointed forward. When capturing insects, the terns hovered briefly and seized prey from the air by slight adjustments with the bill and head. Flight was nearly uninterrupted. After capture, birds returned to their original flying height and repeated the action. Prey taken in this manner, as observed with the spotting scope on 40x, were

mayflies (Ephemeroidea) and damselflies (Zygoptera).

Foraging Behavior of Juveniles

Feeding methods of the juveniles differed from adults. The most recently fledged young, with a totally gray, downy head, foraged by swimming and picking insects from the water and air at a frequency of 40/minute. I observed this on 3 separate occasions for a total of 2 hours. Older juveniles were distinguished by black "ear" patches. One walked on the algae mat and seized insects from the surface for 20 minutes on one occasion. The oldest juvenile observed foraging had a black eye line. It hunted ^{in a manner} similarly ~~to~~ to the adults, by contact dipping on the algae mat, but I was unable to determine success and frequency of its captures.

Wind and Temperature

When wind direction was noted, all birds flew against the wind while dipping and plunging. Plunging birds also appeared to hover more when the wind was stronger.

Temperatures ranged from lows in the 40's ("F) to highs in the afternoon in the 80's. Temperature was usually 75-82 °F during mid-day.

Activity Pattern

The general foraging activity pattern was bimodal with peaks from 0700-0900 \pm 1 hour and 1700-1900 (Figs. 3 and 4), in all areas. Area A was combined with Areas B and C. Area D was 3.8 km long and was combined with the irrigation ditches to the east and the channel between the sumps.

In both areas, contact dipping made up the bulk of the foraging activity (Table 1). During the early morning hours, the number of birds surface plunging was significantly greater than those contact dipping in both areas ($X^2=29.81$, 6 d.f., $P<0.001$ and $X^2=104.06$, 7 d.f., $P<0.001$, respectively).

Efficiency and Frequency

Overall efficiency and frequency of the 3 methods varied greatly from

one another (Table 2). Efficiency of contact dipping also differed significantly at different times of the day ($X^2=12.72$, 2 d.f., $P<0.01$; Table 3). The frequency and efficiency of dipping was highest at mid-day and lowest in the evening. Frequency values were significantly different from morning to afternoon ($t=2.95$, 52 d.f., $P<0.01$) and afternoon to evening ($t=3.87$, 4 d.f., $P<0.001$), but not significant from morning to evening ($t=1.59$, 87 d.f., $P>0.01$).

Light Intensity

Light intensity values around sunrise ranged from 12 lux at 0510 to 24,800 lux at 0610. The mean value at which birds began their activity was 64 lux ($R=44-87$, $n=4$). The light reading around sunset ranged from 9816 to 27 lux from 2030 to 2130, respectively. The mean value at which terns terminated their activity was 67 lux ($R=27-138$, $n=5$).

Aggression

Intra-specific aggression was noted on 28 occasions for a total of 50 chasing episodes. Of the total chases, 14% occurred when one bird had a fish and was pursued by another. Two different identifiable birds accounted for 36% and 20% of the chasing at the two pumphouses. There seemed to be an area around the inflows of 100 m^2 that was a territorial type space defended by an individual bird, when that individual was present. Chasing activity appeared to significantly decrease foraging activity by these birds:

Inter-specific aggression with California gulls (Larus californicus) and ring-billed gulls (Larus delawarensis) affected hunting success of terns. Of 27 observations of inter-specific aggression, 85% occurred with gulls. Other inter-specific encounters occurred with the red-winged blackbird (Agelaius phoeniceus), gadwall (Anas strepera), barn swallow (Hirundo rustica), and great egret (Chasmerodius albus) at Tulelake and with the black tern

(Chlidonias nigra) at Lower Klamath.

Caloric Intake

Fish species available as prey for Forster's tern at Tulelake are listed in Table 4. Partial insect prey available is given in Table 5. Prey observed taken were damselflies (Coenigrionidae), mayflies (Ephemeroidea), and, on one occasion, a dragonfly (not identified to family). The fresh weight of 6 damselfly specimens totalled .3950 grams. The fresh weight of 44 mayfly specimens totalled .4823 grams.

DISCUSSION

Foraging Methods

Forster's terns use specific feeding methods but seem to be able to vary them with variation in prey and environmental conditions. Previous studies on other tern species report that, although most predominantly capture fish, they can switch to other prey species according to availability and need (Bent, 1921; Hawksley, 1957; Ashmole, 1968). This is expedient for an animal requiring high energy intake per day primarily due to foraging methods and high metabolic rate. The time and energy requirements of searching, in addition to existence requirements, must be obtained from the feeding activity. With greater foraging costs, more or better quality food must be procured. Thus, through natural selection, species theoretically optimize foraging strategies to maximize caloric intake with the least time and effort (Emlen, 1966, 1968).

At least two possible explanations exist for the variation of feeding methods of Forster's terns at Tulelake. Tulelake could be a highly optimal environment for the terns. Several feeding areas lie within 6.4 km of the roosting area (Area D), and possibly searching time is not great. With a variety of available prey species, if one is not easily found, the

predator can perhaps switch to alternative food types. This characterizes a patchy environment, defined by MacArthur and Pianka (1966) as an area in which prey species are not located in the proportion in which they occur, i.e. they are clumped. Thus, by behaving as an opportunist, the tern maximizes its food intake. Another possibility is that fish are the preferred species in the diet, but their density is not enough to support the tern population at this time. For the past two years, up to 200 terns fed at one pumphouse at different times during the day (D. G. Raveling and R. Pimentel, pers. comm.). Maximum numbers observed during this study were 6 at any one pumphouse. Up to 10-15 fished in the channel or over pelicans, but not at the inflow areas. Searching time might be greatly increased due to low prey densities. As specialists, they might not be able to obtain adequate calories from fishing, so they are forced to use alternate food sources. Further investigation and records of searching time are needed to evaluate these possibilities.

Foraging of Juveniles

The foraging behavior of juveniles was expected to differ from adults. It takes 9-10 months for the birds to reach their adult plumage and possibly adult feeding patterns. During this time, they are learning prey capture techniques. Recher and Recher (1969) observed differences in foraging success of adult and immature little blue herons (Florida caerulea), which are applicable to several species. Buckley and Buckley (1974), examined differences between adult and juvenile royal terns (Sterna maxima). Both found the young usually had a lower capture rate and were more indiscriminate about what was edible. The youngest immature mouthed detritus, feathers and leaves, as well as insects. In this manner it learned relative palatability of foods without the energetic costs of its probably

inefficient flight. I did not observe feeding of juveniles by adults. I did observe juveniles begging quite frequently and it is possible they were fed. In 27 occasions of begging with adult birds, 52% were followed by one adult feeding the other. The rates could be even higher for juveniles. Feeding of juveniles by adults is undoubtedly very important for growth and maintenance of young birds.

Effects of Wind and Temperature

Wind conditions affected the foraging methods of terns. Wind velocity is lowest just above a surface and increases quickly as height above the surface increases. Flying low into the wind while contact dipping gives less resistance and therefore costs less. Returning high, soaring with the wind, provides an additional energy savings. While surface plunging, the wind resistance holds the tern in place without flapping its wings, while hovering. Salt and Willard (1971), stated that hovering was more efficient in terms of searching ability but energetically more costly than continuous flight. I observed more hovering in windier conditions. This could be due to an increased caloric benefit of higher success balancing the costs of hovering, but only when windy. Salt and Willard (1971) did not believe wind affected efficiency. Dunn (1973a) believed winds were a favorable factor influencing success. I did not note any differences in success rates.

Temperature affects both prey and predator. Prey species are affected in terms of activity and distribution. Temperature increases in the middle of the day. This could lead to a lower oxygen-holding capacity of water as it warms. Warming would occur quickly in shallow waters like those at Tule lake. However, the high amount of surface covered by algae mats and corresponding photosynthetic production of oxygen would counteract this effect. Temperature has a more important effect on the fish. Chubs have a high tolerance for low oxygen levels but a low tolerance for high temperatures.

(Moyle, 1976). They might move to an area of deeper, cooler water where they are harder to spot by feeding terns. In the evening, as temperatures drop, fish move into the shallower water and become more visible to the birds. Insect activity increases at mid-day due to stimulation by higher temperatures, and is lower in the morning and evening.

Temperature will also affect the terns. On several days when the temperature was above 78 °F, I observed birds panting while sitting. This could indicate increased energy expenditure for thermoregulation during mid-day.

Activity Pattern

The bimodal activity pattern is exhibited by many birds and mammals (Harker, 1950). This pattern is probably due to several factors, one of which is the energy deficit occurring overnight, necessitating a morning feeding period to replenish energy reserves. An evening feeding period allows the terns to have a positive energy balance overnight and may assist in thermoregulation. The mid-day lull is often seen, having its basis in part on increased energetic expenditure of flight during warmer times of the day and in part on endogenous rhythms (Aschoff and Pohl, 1967). With terns this activity pattern may also have significance in terms of prey accessibility and ease of capture. It is possible that, in the morning, certain light intensities stimulate fish activity (Schere~~r~~, 1976). Due to prey availability, terns would forage at that time. In the afternoon, the fish could be harder to find and the cost of searching greater. ^{possibly} Insects would become more accessible.

Efficiencies and Frequencies

The differences in efficiencies and frequencies of various feeding methods are expected. Insects, the prey species captured by dipping and hawking,

are smaller than fish captured by plunging. A greater number of insects must be captured to make hunting of them worthwhile. It is possible, since insects are on or just above the surface of the water and often in dense groupings, that they are easier to see than fish. Chubs in Tulelake do not school except where artificially concentrated at pumphouses, and are more evenly dispersed throughout the area (Moyle, 1976). Although the efficiency of plunging is lower, the caloric return per capture is undoubtedly greater. Wright (1909) described artic terns (Sterna paradisea) feeding on mayflies. Mayflies are very small and the caloric return per capture is quite low. Benefits of mayfly capture are not immediately apparent. However, this activity occurred on only one day when the flies appeared in large numbers in a centralized location. Efficiency of capture was extremely high and searching costs were not great.

Differences in efficiency of contact dipping at different times of the day can be explained in several ways. Efficiency and frequency for morning hours are not significantly different from overall values, but they are lower than mid-day. In the morning insects might be sluggish, easier to catch, but harder to detect, thus decreasing the efficiency and capture frequency when compared with mid-day feeding. Evening capture rates are lower than mid-day possibly due to a lessening of insect activity. Thus, it appears terns might detect their prey by motion.

Light Intensity

Effect of light on activity patterns has been discussed in several species; Canada geese (Branta canadensis) by Raveling, et. al. (1972), ducks (Anas spp.) by Brackbill (1952), and artic terns by Hawksley (1957). Light appears to be important in regulating activity of Forster's tern.

Light intensity changes rapidly around sunrise and sunset as indicated by the ranges presented in the data. Terns responded to specific intensity differences in a period of 5-10 minutes. Both initiation and cessation of activity occurred near the same mean lux value. This probably indicates a high specificity for light intensity regimes. This could be due in part to prey movement and accessibility and also to endogenous circadian rhythms with light as a zeitgeber (Aschoff and Pohl, 1967).

Caloric Intake

National Academy of Sciences (1973) and Cummins and Wuychek (1971) determined the average caloric value of cyprinid fish species to be 1.49 kcal/g fresh weight. An average 3 gram fish of the species taken, Tui chub and blue chub, has an approximate caloric value of 4.47 kcal. At a capture frequency of 20 attempts/hour with 32% success, 6.4 fish/hour are taken. This gives a value of 28.60 kcal/hour. Dunn(1973) indicates 82% assimilation efficiency ($\frac{\text{Metabolizable energy}}{\text{Ingested energy}} \times 100$) for fish. This gives a value of 23.45 kcal/hour of available energy.

Caloric values for damselflies, determined from the same sources, have a fresh weight value of 0.767 kcal/gram, equivalent to 0.065 kcal/individual. At a dipping frequency of 354 attempts/hour with 83% success, a tern could catch 293 individuals/hour. At 66% efficiency of digestion for insects (Gibbs, 1957), the caloric return is 12.5 kcal/hour.

Mayflies had a caloric value of .700 kcal/gram fresh weight, equivalent to 0.008 kcal/individual. At a capture rate of 660 attempts/hour and 100% capture efficiency, the hourly intake was 7.26 kcal. Again at 66% assimilation efficiency, available energy was 4.79 kcal/hour.

Energy Expenditure

Basal metabolic rate (BMR) was estimated according to King and Farner

Ashoff & Pohl formula?

(1961). The formula used was $BMR = 74.3 W^{.744}$ kcal/day (W=weight in kilograms). By dividing by 24, I got an hourly caloric expenditure of $3.09 W^{.744}$. Using a mean tern weight (uncorrected for stomach contents) of 146 grams, or .146 kilograms (Baltz, unpublished data), I determined BMR to be 0.74 kcal/hour. Existence metabolism is $3.4 \times BMR$ (King, 1973) and energy requirements for flight are $12 \times BMR$ (LeFebvre, 1964). This gives caloric output of 2.52 kcal/hour and 8.88 kcal/hour, respectively. By estimating activity of an average tern from Figs. 3 and 4, an approximate daily caloric intake and possible daily caloric expenditure were obtained (Table 6). Costs of thermoregulation, reproduction and molt were not considered so actual output of energy is probably greater. Caloric intake might be altered by several factors such as the actual values of the food items, other possible food types not included in the estimation or different frequency and efficiency values.

From the data, however, it appears that Forster's terns at Tulelake obtain maximum calories per energy expended in foraging by using different types of prey, foraging at optimal times of day and foraging in areas where prey is relatively abundant. Weather and light are also important factors regulating foraging efficiency and success in the Forster's tern.

LITERATURE CITED

Ashoff, J. and H. Pohl. 1967. Circadian rhythms in birds. Proc. Inter. Ornithol. Congr. 14:81-106.

Ashmole, N. P. 1968. Body size, prey size and ecological segregation in five sympatric species of tropical terns (Aves: Laridae). Syst. Zool. 17:292-304.

_____ 1971. Sea bird ecology and the marine environment. In ^{pp 223-286}

- D. S. Farner and J. R. King (eds.). Avian Biology. Vol. 1. Academic Press, New York.
- and M. J. Ashmole. 1967. Comparative feeding ecology of seabirds of a tropical oceanic island. Peabody Mus. Nat. Hist., Yale Univ. Bull. 24:1-31.
- Begg, G. W. 1973. The feeding habits of the White-winged black tern on Lake Karila. Ostrich 44:149-153.
- Bent, A. C. 1921. Life Histories of North American gulls and terns. Dover Publ., Inc., New York. 337 pp.
- Brackbill, Hervey. 1952. Light intensity and waterfowl flight: preflight activities. Wil. Bull. 64:242-244.
- Buckley, F. G. and P. A. Buckley. 1974. Comparative feeding ecology of wintering adult and juvenile royal tern- (Aves: Laridae, Sterninae). Ecology 55:1053-1063.
- Cummins, K. W. and J. C. Wuychek. 1971. Caloric equivalents for investigations in ecological energetics. Internat. Vereinigung fur Theoretische und Angewandte Limnologie 18:1-37.
- Dunn, E. K. 1973a. Changes in fishing ability of terns associated with windspeed and sea surface conditions. Nat. 244:520-521.
- 1973b. Energy allocation of nestling double-crested cormorants. Ph. D. thesis, Univ. of Michigan.
- Emlen, J. M. 1966. The role of time and energy in food preference. Amer. Nat. 100:611-617.
- 1968. Optimal choice in animals. Amer. Nat. 102:385-389.
- Gibb, J. A. 1957. Food requirements and other observations on captive tits. Bird Study 4:207-215.
- Harker, J. E. 1958. Diurnal rhythms in the animal kingdom. Biol. Rev. 33: 1-52.

- Hawksley, O. 1957. Ecology of a breeding population of arctic terns.
Bird Banding 28:57-92.
- King, J. R. 1973. Energetics of reproduction in birds. pp. 78-110. In
D. S. Farner (ed.). Breeding Biology of Birds: Proceedings of Symposium
on Breeding Behavior and Reproductive Physiology in Birds. Nat. Academy
of Sciences. Washington D. C.
- 1974. Seasonal allocation of time and energy resources in birds,
pp. 1-85. In R. A. Paynter (ed.) Avian Energetics. Nut. Ornith. Club 15.
Cambridge, Mass.
- and D. S. Farner. 1961. Energy metabolism, thermoregulation and
body temperature, pp. 215-288. In A. J. Marshall (ed.). Biol. and Comp.
Phys. of Birds. Vol II. Academic Press, New York.
- LeFebvre, E. A. 1964. The use of D_2O^{18} for measuring energy metabolism in
Columbia livia at rest and in flight. Auk 81:403-416.
- MacArthur, R. H. and E. P. Pianka. 1966 On optimal use of a patchy environ-
ment. Amer. Nat. 100:603-609.
- Moyle, P. B. 1976. Inland fishes of California. Univ. of Calif. Press.
Berkeley. 405 pp.
- National Academy of Sciences. 1973. Nutrient requirements of trout, salmon,
and catfish. Nutrient Requirements of Domestic Animals 11:35-36.
- Orians, G. H. 1971. Foraging behavior, ^{pp. 313-314.} In D. S. and J. R. King (eds.).
Avian Biology. Vol. I. Academic Press. New York.
- Pearson, T. H. 1968. The feeding ecology of seabird species breeding on
the Farne Islands, Northumberland. J. An. Ecol. 37:521-552.
- Raveling, D. G., W. E. Crews, and W. D. Klimstra. 1972. Activity patterns
of Canada geese during winter. Wils. Bull. 84:278-295.
- Recher, H. F. and G. A. Recher. 1969. Comparative foraging efficiencies

- of adult and immature little blue herons (Florida caerulea). Anim. Behav. 17:320-322.
- Ricklefs, R. E. 1974. Energetics of reproduction in birds, pp. 152-292. In R. A. Paynter (ed.). Avian Energetics. Nut. Ornith. Club 15. Cambridge.
- Salt, G. W. and D. E. Willard. 1971. The hunting behavior and success of Forster's tern. Ecol. 52:989-998.
- Scherer, E. 1976. Overhead light intensity and vertical positioning of the walleye (Stizostedion vitreum vitreum). J. Fish Res. Board. Can. 33: 289-292.
- Schoener, T. W. 1971. Theory of feeding strategies. Ann. Rev. Syst. Ecol. 2:369-404.
- Wright, W. C. 1909. Artic terns feeding on crane and mayflies. Brit. Birds 3:91.

FIGURE LEGENDS

Figure 1. Tulelake National Wildlife Refuge Study Area

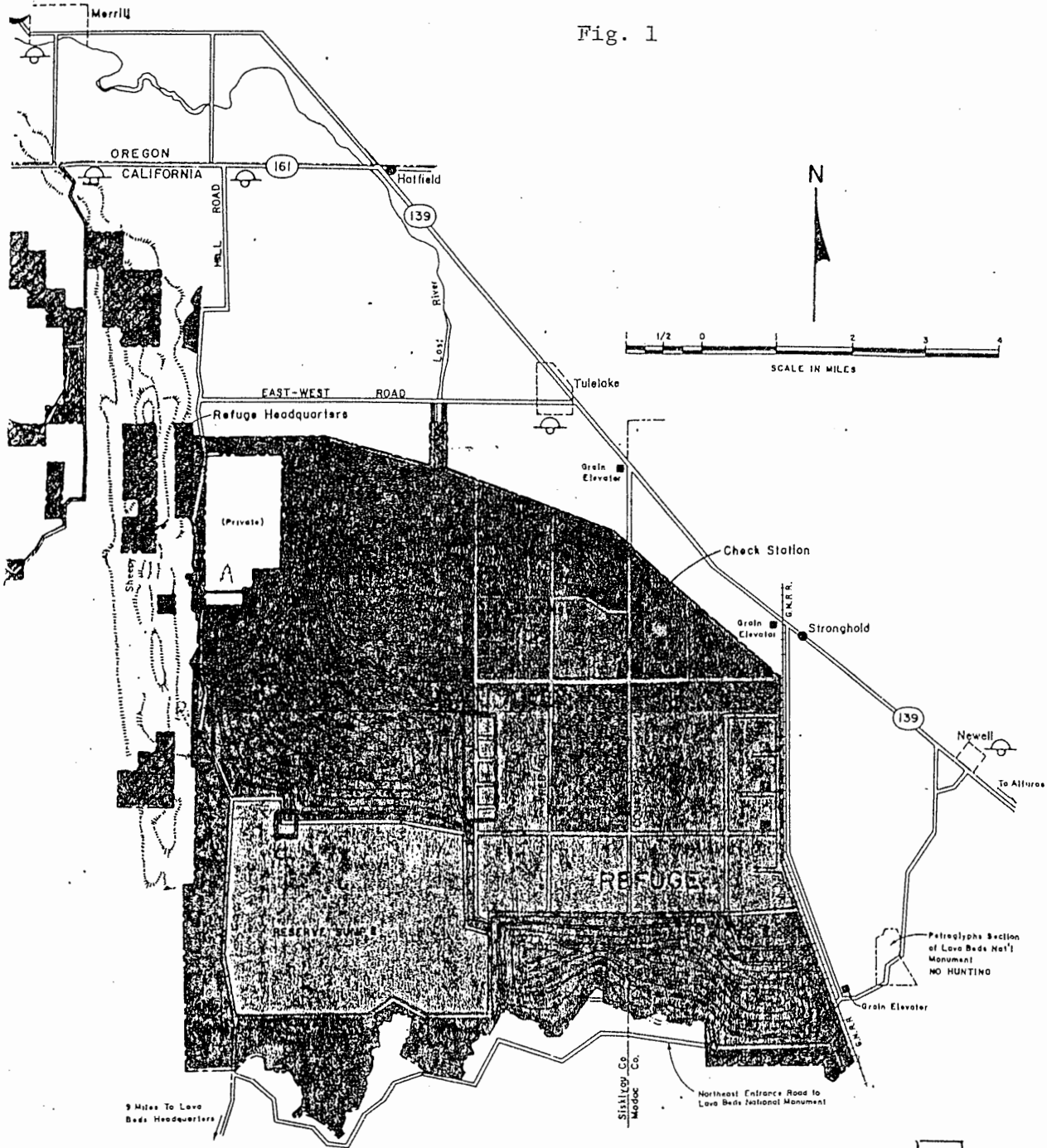
Figure 2. Lower Klamath National Wildlife Refuge Study Area

Figure 3. Numbers of Forster's terns seen foraging at Tulelake in study areas A, B, and C. Horizontal bar is \bar{x} ; vertical bar indicates range; hatched box is 2 standard errors.

Figure 4. Numbers of Forster's terns seen foraging at Tulelake in study area D.

Don't need
explanation
both here & on
Figure -
one on the
other

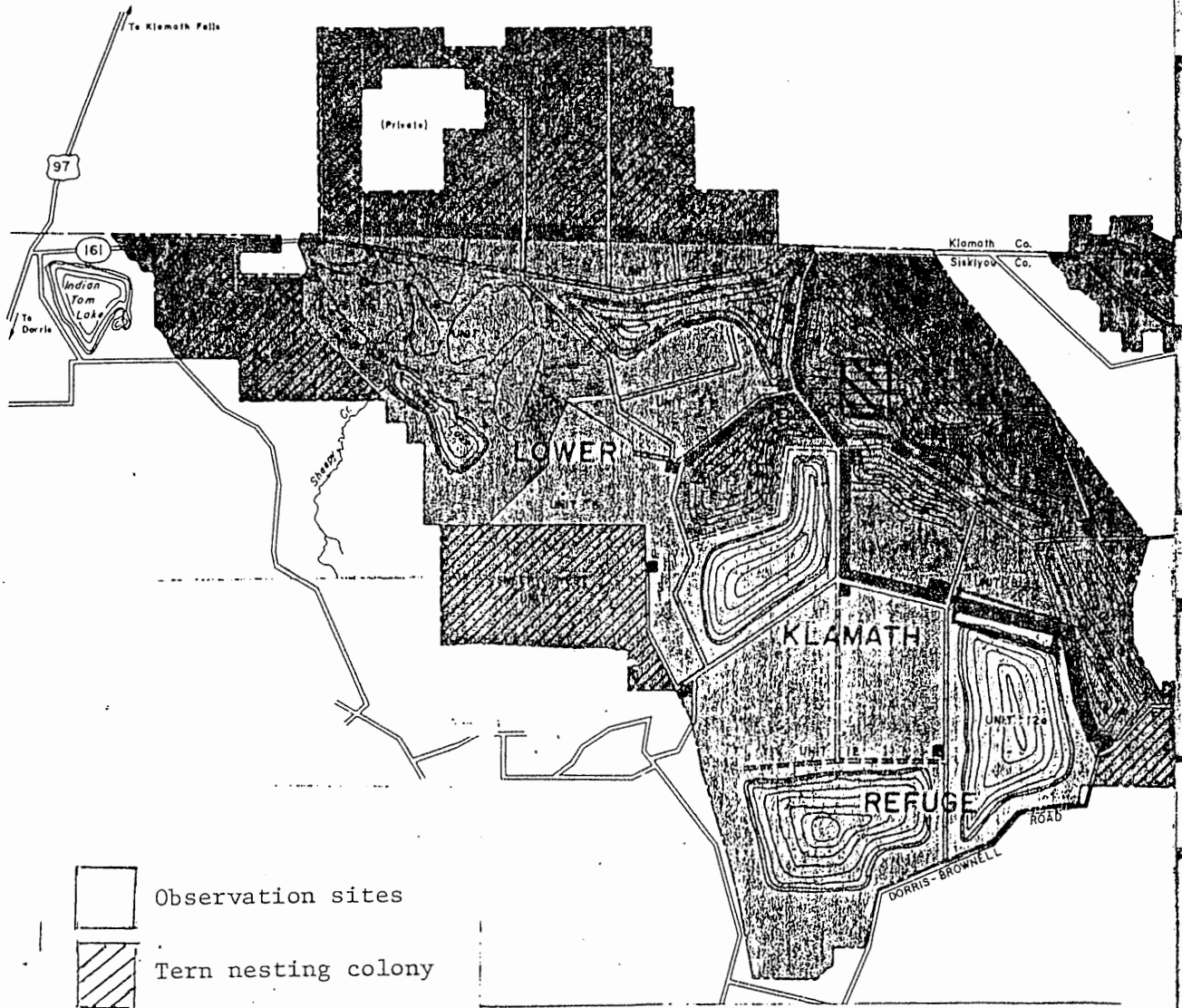
Fig. 1



9 Miles To Lava Beds Headquarters

□ Observation sites

Fig. 2



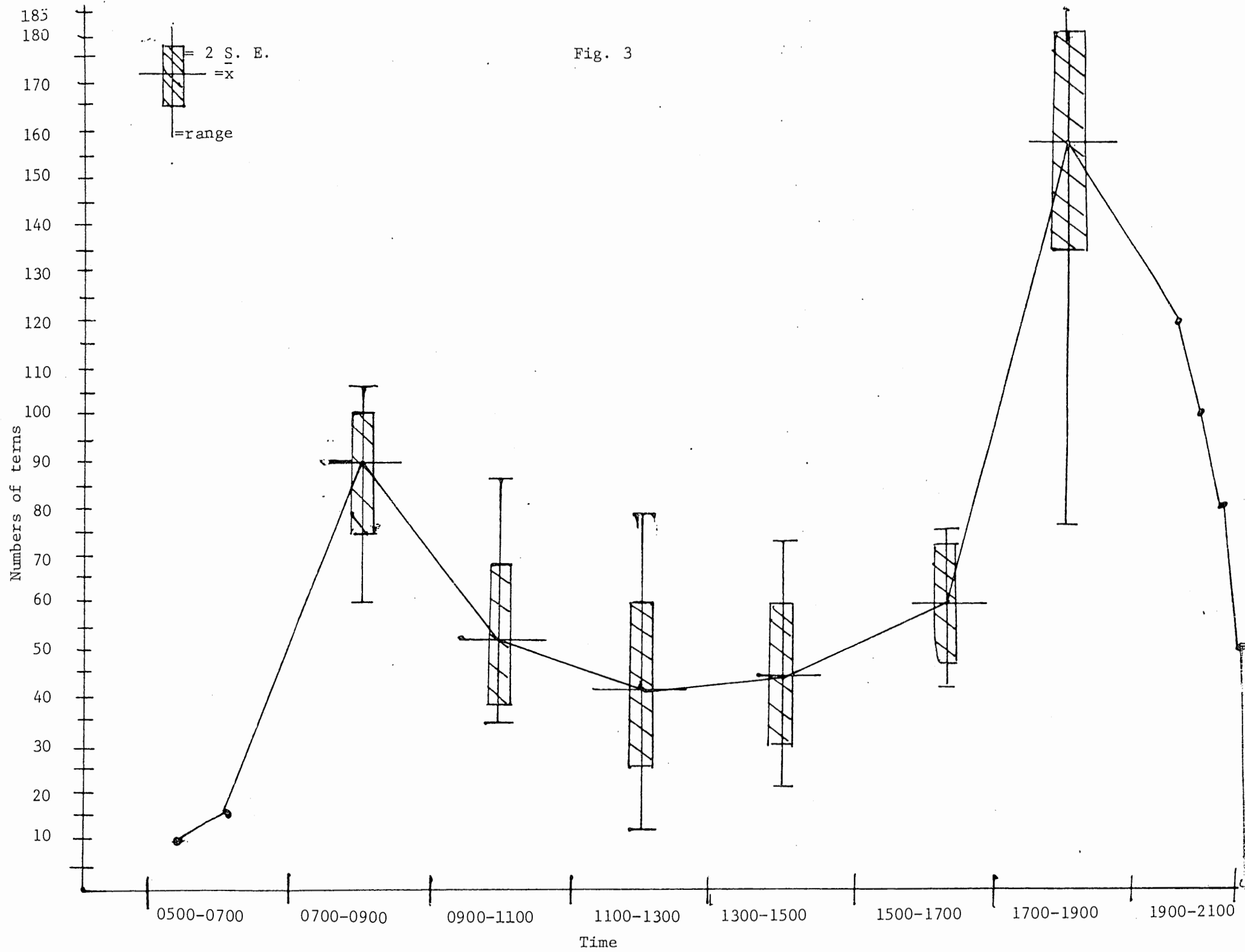
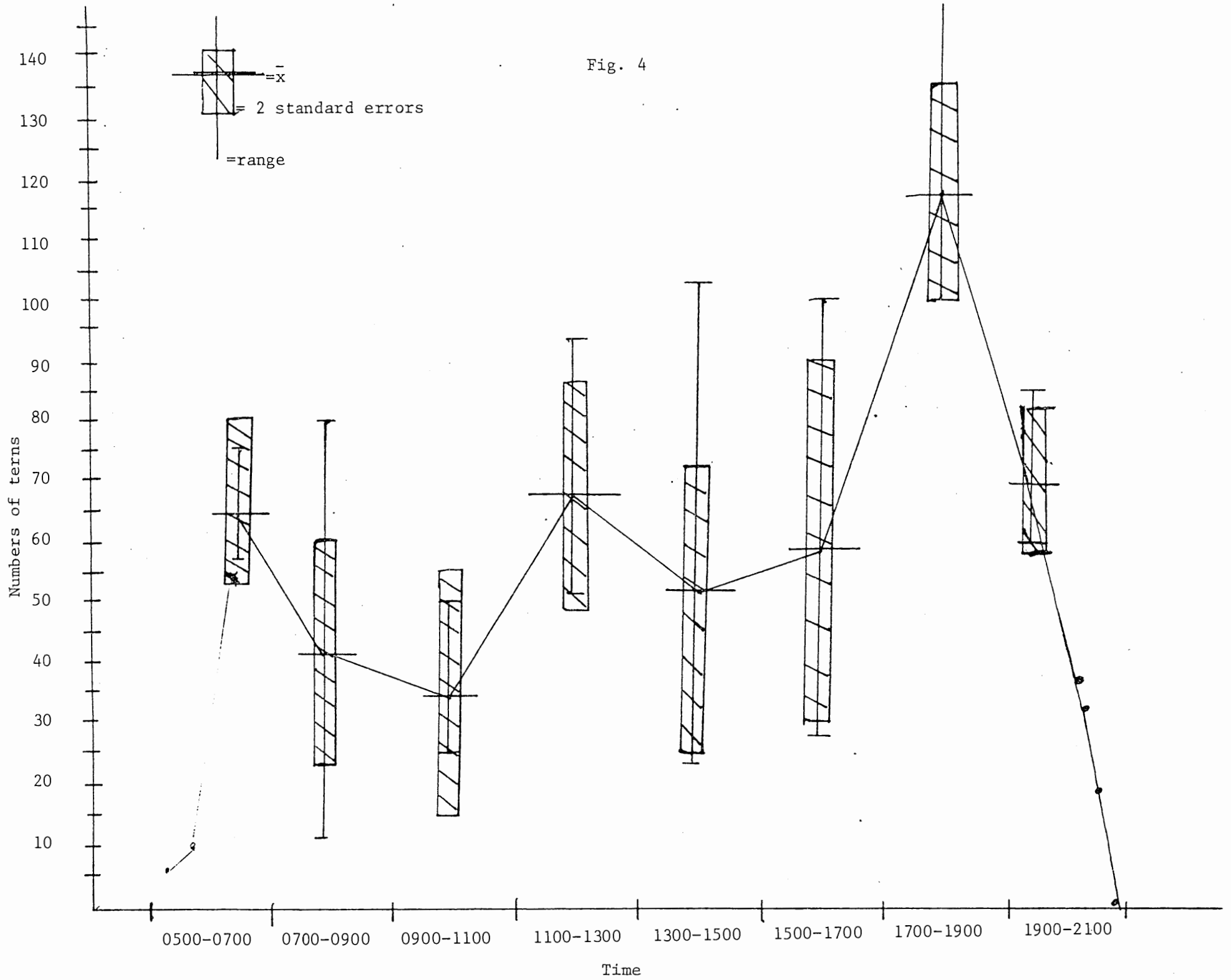


Fig. 4



For. terns

Table 1. Mean numbers of birds foraging by different methods at different hours of the day.

Time of day	Foraging Method					
	Mean numbers of birds observed		Contact dipping (%)		Surface plunging (%)	
	<u>Area A</u>	<u>Area D</u>	<u>Area A</u>	<u>Area D</u>	<u>Area A</u>	<u>Area D</u>
0500-0700	13 R=10-15 n=2	65 R=55-75 n=2	46	28	54	72
0700-0900	90 R=60-105 n=5	40 R=10-80 n=4	89	83	11	17
0900-1100	53 R=35-85 n=6	35 R=25-50 n=2	84	43	16	20
1100-1300	41 R=15-80 n=8	67 R=50-93 n=4	71	93	29	7
1300-1500	45 R=23-73 n=6	52 R=28-93 n=6	93	70	7	11
1500-1700	60 R=45-75 n=5	57 R=26-100 n=6	93	88	7	12
1700-1900	156 R=75-240 n=6	107 R=100-155 n=3	99	89	1	5
1900-2000	115 R=85-120 n=3	70 R=55-85 n=2	93	100	7	—
2000-2100	39 R=4-130 n=9	—	100	—	—	—

Table 2. Success rates and frequency of three feeding methods of Forster's terns

Feeding Method	Total Observations	$\bar{x} \pm SE$ Minutes of Observations	Total Attempts	Success (%)	Frequency of Activity in Attempts/Hour
Contact Dipping	151	3.8 ± 0.16	3441	83	354 R=18-1860
Surface Plunging	67	10.41 ± 1.24	227	32	20 R=1-48
Hawking	29	1.16 ± 0.07	367	100	660 R=480-1200

Table 3. Success rates and frequency of contact dipping at different times of the day.

Time of Day	Total Observations	Minutes of Observations $\bar{x} \pm SE$	Total Attempts	Success (%)	Frequency of Activity in Dips/Minute $\bar{x} \pm SE$
0700-1000	66	3.7 ± 0.27 R=1-10	1264	80.5	5.89 ± 0.54 R=0.4-22
1200-1500	36	3.9 ± 0.37 R=1-11	1177	84.4	8.73 ± 1.07 R=1-31
1700-2000	27	3.17 ± 0.39 R=1-10	399	76.9	4.69 ± 0.45 R=1-10

Table 4. Fish species present in Tulelake in order of abundance.

Common Name	Scientific Name
Tui chub ¹	<u>Gila bicolor</u>
Dace	<u>Rhinichthys spp.</u>
Blue chub ¹	<u>Gila operulea</u>
Large scale sucker	<u>Catostomus snyderi</u>
Yellow perch	<u>Perca flavescens</u>
Lost River sucker	<u>Catostomus luxatus</u>
Short-nosed sucker	<u>Chasmistes brevirostris</u>
Brown bullhead catfish	<u>Ictalurus nebulosus</u>
Small mouth bass	<u>Micropterus dolomieu</u>
Yellow catfish	<u>Ictalurus natalis</u>
White sturgeon	<u>Acipenser transmontanus</u>

Courtesy of Ed O'Neill (13 July, 1977)

¹Species observed taken

Table 5. Partial insect prey available at Tulelake. (6 July, 1978)

Common Name	Order	Family
Damselfly ¹	Odonata	Coenagrionidae
Adults		
Naiads		
Dragonfly ¹	Odonata	
Long-legged fly	Diptera	Dolichopodidae
Black fly	Diptera	Simuliidae
Mayfly ¹	Ephemeroptera	Ephemeridae
Water-boatman	Hemiptera	Corixidae
Back-skimmers	Hemiptera	Notonectidae

¹Species observed taken by Forster's terns.

Table 6. Estimated daily energy budget for different activities of Forster's tern.

Time	Activity	Caloric Intake in kcal	Caloric Output in kcal
0500-0800	Plunging	70.35	34.2
0800-1300	Dipping	62.5	57.0
1300-1500	Resting	0	5.04
1500-2100	Dipping	75	68.4
2100-0500	Resting	<u>0</u>	<u>20.16</u>
Total		207.85	184.8