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How does seasonal variation in the fledging mass of Cassin's Auklet (*Ptychoramphus aleuticus*) chicks relate to seasonal variation in parental quality?

Recently, modeling in ecology has taken a major shift towards models that 'create' each and every individual in an ecological system in order to generate the dynamics of that system (Judson 1992). Traditional general models in ecology tend to ignore two fundamental aspects of biology that all individuals are different, and that interactions between individuals take place locally (DeAngelis and Gross 1992). Most importantly from an evolution perspective, individuals are units of selection (Lomnicki 1988). Furthermore, the boundry between an individual and its environment is usually clear, therefore an individual is usually easier to define than an ecosystem or a species (Lomnicki 1988). Models that follow individuals should be able to delve deeper into the complex behaviours of ecosystems, therefore generating a greater understanding of some of the dynamics of ecological hierarchies beyond interactions among individuals (Huston et al. 1988).

Traditionally, studies of seabird population ecology have used the average or mean performance of a population to estimate population growth, fecundity, and survival. Although means are sometimes useful for characterizing population dynamics, they are of limited use in examining life history questions in which individual variation is so great that many individuals are not representative of the population mean (Pierotti and Annett 1995). In recent studies in seabird population ecology, the emphasis has been

placed on variation in individual quality as it relates to behavioural ecology (Monaghan and Parrish per comm). Models based on individual variation allow differences in an individual's sex, age and quality to be taken into account.

Ydenberg (1989) dynamic fledging model predicts that fledging mass often declines with fledging date (does occur in some colonies and years, Birkhead and Nettleship 1982; Harris 1982; Vermeer 1987). This model of nest departure decision incorporates the differential growth benefits and mortality costs of pre- and postfledging habitats; nest and ocean. The most basic prediction of the model is the existence of a negatively inclined fledging boundary in mass-time space: nestlings fledge as their growth trajectory hits the boundary. As a consequence, the model predicts that early hatched nestlings are faster growing, fledge younger and heavier than later-hatched nestlings which fledge older and lighter. This pattern has usually been attributed directly to a seasonal decline in growth rates due to the delayed breeding of poorer quality parents and/or late in the season a decline in the availability of food to feed nestlings (Hatchwell 1991; Lack 1966). Does a chick's fledging mass vary in relation to the mass of the parents? If a chick fledges at a low fledging mass, is it adaptive for the individual to make-up for this growth decline later in life by 'catching up' with compensatory growth or is the individual permanently stunted in its growth? The low fledging mass may be caused by lack of food or because it had a small genotype which produced a small phenotype.

In the alcids, different nestlings in the same colony may have markedly different masses at hatching, may hatch at different

dates, and may experience different growth profiles in the nest. In intermediate and semiprecocial species in the alcid family numerous studies have shown substantial intraspecific variation in the timing of fledging, fledging mass and age at fledging. For example, in Rhinoceros Auklets fledging mass varies from 45% to more than 80% of mean adult body mass, and age at fledging varies between 40 and 70 d (Vermeer and Cullen 1979; Wilson and Manuwal 1986; Harfenist 1991). In addition, many researchers have documented decreases in fledging mass of chicks the later in the season the chick fledges (Hedgren and Linnman 1979; Manuwal 1979; Sealy 1981; Birkhead and Nettleship 1982; Harris 1982; Gaston et al. 1983; Vermeer 1981, 1987).

Various hypotheses have been put forward to explain this seasonal growth rate decline. Components of the first five hypotheses; age, size, egg size, adaptive adjustment, and hatching mass could be considered to be related to parental quality.

1) *Young inexperienced birds breed later.* Hatchwell (1991) supports this hypothesis with the following observational and experimental evidence on Common Murres (*Uria aalge*): a) naturally late breeders provisioned nestlings at a lower rate, b) experimentally delayed clutches had greater reproductive success than naturally late clutches, and c) age-specific size was the same between experimentally delayed clutches and early control clutches. The 1994 Triangle Cassin's Auklet mark/recapture data showing an increased capture rate of young, breeding birds (brown-eyed birds with full brood-patches) later in the breeding season, is consistent with this theory.

2) *Seasonal decline in adult size.* Adult size influences the chick's growth rate because of the relationship between the size of the adult and the size of the food load the adults are able to deliver to the chick (Gaston 1985).

3) *Seasonally declining egg size.* A nestling may be constrained to a certain growth trajectory by egg size (Hedgren and Linnman 1979). A decline in egg volume relating to laying date has been demonstrated in: Thick-billed Murres (*Uria lomvia*) (Birkhead and Nettleship 1982), Atlantic Puffin (*Fratercula artica*) (Harris 1980), Razorbills (*Alca torda*) (Lloyd 1979), Gannets (*Sula bassanus*) (Nelson 1966), and Black Guillemots (*Cepphus grylle*) (Cairns 1987). Perrins (1970) believed egg size could be constrained by food availability or parental quality at the time of egg production.

4) *Seasonal adaptive adjustment.* Provisioning rates and the timing of breeding may be adjusted by parents in an adaptive way to maximize their reproductive success. In Common Murres, chicks from eggs hatched before median laying date and nestlings fledging later than median fledging date experienced a greater mortality rate (Hatchwell 1991). Adjusting ones fledging age to be more synchronous with the rest of the colony (Hatchwell 1991) may be important to a) forage successfully, since colonies may act as information centers allowing foragers to inform others where to find food (Hedgren and Linnman 1979) and b) lessen predation risk by creating a dilution effect (Daan and Tinbergen 1979). Gaston (1985) proposed that late in the season nestling may have a lower value to their parents in terms of fitness, therefore parents may reduce their effort. Ydenberg (1989) and Ydenberg et al. (1995) indicated that

late nestlings may have a lower fitness, since the time they have to grow to adult size is limited at the end of the season.

5) *Seasonally declining hatching mass*. The mass at which a nestling hatches may constrain it to a particular growth trajectory (Gaston 1985; Birkhead and Nettleship 1982).

6) *Seasonal decline in food quality or availability*. (Lack 1966).

Aims

i) To relate chick growth strategies/patterns to phenotypic variation in adults (eg. adult body size) and measures of parental quality.

-using 'conventional' quality measures eg. mass, structural size.

-using 'novel' methods eg. blood parameters, parasite load.

ii) Potential covariation between parental provisioning ability and quality per se will be investigated by cross-fostering experiment.

By cross-fostering chicks I will be able to investigate the heritability of size independent of parental quality in provisioning/chick rearing.

Further components of the alcid breeding cycle (unusual in other birds) will also be considered, which may influence or reflect parental quality, chick rearing ability and hence fledging age/mass.

iii) Programed mass loss has been demonstrated in various small alcids. This adaptive mass loss is thought to lessen wing-loading during the chick-provisioning period. Therefore high mass, which has been used traditionally as an indicator of quality in breeding birds may not be appropriate in Cassin's Auklets.

iv) The moult-breeding overlap of Cassin's Auklet parents and its consequences for chick growth will be investigated. As the parents begin to molt their primaries, wing-loading increases. This

increased energetic demand on the adults may have a direct effect
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on the chick's growth via the parent's provisioning ability. There may also be an indirect effect on chick growth via the energy expended by the adults in the regrowth of their molted feathers. The possibility of seasonal 'selection' to complete molt will be examined. A possible scenario is as follows: Late breeding birds will face greater selection to molt faster, which would increase energy consumption and wing loading, therefore late breeders would have poor parental ability causing lower chick growth.

By addressing these questions, I will be better able to quantify to what extent the various hypothesis put forward earlier in the paper explain the phenomena of seasonal variation in the fledging mass of alcid chicks.

Phenotype variation/parental quality

By collecting morphological data (tarsus, culmen, bill depth, wing length, body mass) on families of Cassin's Auklets I will attempt to correlate the parent's structural size and mass with that of the chick at fledging, to try to explain changes in fledging mass as the breeding season progresses. Explanations of a correlation between the parent's structural size and mass with that of the chick could be explained if mass is a high heritable or if the parents and the chick developed in similar environments or a combination of the two. Does having a certain phenotype ie. having a particular body size; have importance in fledging a chick of a certain size?

One hypothesis put forward to explain the seasonal fledging decline of alcid chicks is that adults that breed later in the season are smaller in structural size than early breeding adults (Gaston

1985). By looking at the variation of parent-offspring phenotypic resemblance in early to late layers I will be able to determine if the size of the breeding adults has an effect on the fledging structural size and mass of the chick. The size of the breeding adults may have an effect on the fledging mass of the chick if the adult's size affects the size of the food load the parent can deliver.

Sexual dimorphism can complicate the analysis of heritability since it may directly affect the estimate and the variation (Wiggins 1989). Nelson (1981) stated that except for a shallower bill of the female or the deeper bill of the male (mean bill depth for females 9.5 mm, n=19; for males 10.9 mm, n=14) , sexual dimorphism is not apparent in Cassin's Auklets. Data in the literature is lacking on measurements of other morphological traits for the different sexes of Cassin's Auklets, therefore I speculate that sexual dimorphism will become apparent for other morphological traits once measurements of parents are carried out. Sexual dimorphic traits cannot be corrected for since offspring can not be sexed.

The analysis of heritability will be further complicated because morphological traits of offspring may not have attained full adult size by fledging time (Garnett 1981). Manuwal (1972) reported on the percentage of adult size attained for three morphological measurements of fledging Cassin's Auklets. Tarsus length of fledgers attained 98% of adult length, followed by wing length of fledging chicks which reached 92% of adult length, and finally the culmen length of fledging chicks only reached 90% of adult length.

In recent years, more and more observers have found that supposed monogamous birds do a great deal of mating outside the

pair-bond, especially in colonial birds. Consequently, one might expect a low father/offspring resemblance within some families, if the female has had its egg fertilized as a result of a mating outside the pair-bond. Therefore, similarities between offspring and parents may be limited to mother/offspring similarities and father/offspring similarities where extra-pair copulations have not occurred. By determining the percentage of similar father/offspring pairs within the families sampled I will be able to indirectly estimate the percentage of successful extra-pair copulations within the population.

Moller and Birkhead (1992) have shown that the frequency of extra-pair paternity can be reliably estimated from sex differences in the heritability of sexually monomorphic morphological traits. The authors estimated the reliability of the heritability method to estimate extra-pair paternity by regressing estimates of extra-pair paternity derived from biochemical methods on estimates of extra-pair paternity derived from the heritability method in eight different bird species. This suggests that the heritability method can be used to obtain reliable estimates of extra-pair paternity in birds.

Cross-fostering Experiment

Studies of the heritability of body size have facilitated investigations of natural selection in natural populations of birds. Many studies from natural bird populations have shown that most morphological traits have large heritables (Brooke 1977; Boag and Grant 1978; Smith and Zach 1979; Garnett 1981), but (Cooch et al. 1993) showed that morphological traits in Lesser Snow Geese can

greatly affected by the abundance of food or the lack there of. Most of these studies were designed to see if the population would respond genetically to current selection, or whether past episodes of selection had eliminated genetic variation.

I propose to investigate heritability of size independent of parental quality in provisioning/chick rearing. It is clear that both genetic and environmental effects may play a significant role in the determination of the body size of the chick. Environmental effects, such as variation in parental quality and maternal effects (possible maternal influence through egg size) may also influence the estimation of parent-offspring resemblance. One way to control for such aspects of parental quality is to cross-foster chicks among broods and compare the size of offspring to both their true and foster parents.

I propose to switch eggs (possibly chicks that hatch on the same date?) laid on the same date between parents of different sizes to control for variation in parental quality and maternal effects. By establishing a pattern of phenotypic variation, I will be able to determine the degree to which it reflects an underlying genetic variation.

Condition

Birds in good condition presumably are better able to both reproduce and survive whereas birds in poor condition may neither reproduce or survive as well. Therefore, the better condition the parents are in, the more likely they will be able to reproduce and survive to reproduce again. Reproductive "decisions", such as timing of laying, size of egg and foraging performance can effect many

aspects of the breeding effort. Since it is likely that reproductive decisions within a breeding season are made with reference to adult body condition, it will be necessary to monitor 'condition' during the breeding season by using various methods of indirectly measuring condition.

Condition of the parents will affect the ability of the parents to provide parental care to their offspring. Parental care, the behaviour which increases the fitness of the parents' offspring ie. provisioning rate, can have a large effect on the survival of offspring after fledging (Wolf et al. 1988) as well as on the offspring's future breeding success if they survive. As parental expenditure (proportion of the parent's resources spent on parental care ie. time and energy) increases, the parental investment (the extent to which parental care of offspring reduces parents' residual reproductive value) also increases. The energetic costs of feeding young are high, peaking at four times BMR, exceeding those of egg production, incubation or gestation (Robbins 1983). Therefore, the condition of the parents should be measured during late chick-rearing and compared with condition indices before chick-rearing begins to estimate parental expenditure.

Over the last 15 to 20 years, ornithologists have sought to devise nondestructive methods to determine physical condition and energy reserves of birds. Both invasive and noninvasive techniques have been investigated, including blood chemistry (LeMaho et al. 1981), labeled water dilution space (Nagy and Costa 1980), fat scoring (Krementz and Penleton 1990), body mass adjusted for morphological measurements (Johnson et al. 1985), ultrasonic

techniques (Baldassarre et al. 1980) and the total body electrical conductivity method (TOBEC) (Roby 1991).

Size-adjusted body mass

Recently, in the scientific literature there has been widespread misunderstanding between two useful and distinct variables: body size and body mass. 'Condition' indices based on size-adjusted body mass have been used commonly in many avian studies.

Piersma and Davidson (1991) define structural size as the "nutrient reserve-independent size of the bird", therefore structural size is independent of the nutritional status that varies with time of day and year, reproductive status, and habitat quality. Wishart (1979) suggested that skeletal mass is almost entirely reserve-independent; and should provide an accurate estimator of structural size on which linear dimensions can be regressed to provide an index of structural size, although Cooch et al. (1993) have demonstrated that structural size can be affected by environmental factors. But, since most skeletal measurements require killing the bird, they are of little help in studies of live birds. Therefore, body-size variation in live birds is usually controlled for in analyses of body mass by the use of one or more easily measured external measurements, usually the lengths of wings, tarsus, body and culmen. Care must be taken in choosing the appropriate external measurements since they may differ interspecifically in how much they correlate with the actual structural size (as measured by skeletal volume) of the species in question.

Birds have a great capacity to vary their mass and volume depending on their nutritional status which allows them to exercise

and to survive periods of negative energy and nutrient balance. Body mass combines information about structural size and nutrient reserve mass but alone can not provide an indicator of structural size.

To study the phenotypic relationship between chick and parent it is likely that structural size would be the variable that is most important. When looking at the quality of the parent in question size-adjusted body mass index would be more appropriate in revealing the 'condition' of the bird.

Measurement Error

Assessment of measurement error is important for studies that use morphometric variables to make statistical inferences about biological phenomena (e.g. studies of adaptive radiation, taxonomic relationships, interspecific competition, age and sex determination, body condition, heritability, and growth). Use of variables with large measurement errors can result in Type 2 statistical errors (ie. accepting false null hypotheses). To assess relative measurement error of several external measures in Cassin's Auklets, repeated measurements will be taken of the skeletal and external components of carcasses found around the island. This will allow me to assess the correlations between the measurements of the external structures of live birds (ie. tarsus, culmen, bill-depth, keel-length) to that of the skeletal measurements of collected carcasses. In other words I will be able to assess the structural size of live birds by using their external morphological structures.

Age effects

To prove that younger birds are breeding later in the season, parents from individual burrows will be divided into two different age classes based on iris colour; brown-eyed breeders will be considered less than three years of age while white-eyed breeders will be considered to be over three years of age. Banding records indicate that approximately 80% of Cassin's Auklets on the Farallon Islands do not breed until they are at least three years old (Manuwal 1978). The 1995 nocturnal Cassin's Auklet banding capture data shows a clear trend, as the breeding season progressed, towards the capture of brown-eyed birds with brood patches. Young birds tend to breed later in the season and since they are relatively inexperienced, they are able to rear fewer young on average than older birds (Coulson and White 1960). However, in long-lived species such as alcids, only a small proportion of the population at anytime will be made-up of young, inexperienced breeders, which suggests that some other factor is important.

Since many of the first-time breeders will be 3 years old and therefore have white eyes; eye colour will not be a good criterion for determining if these 3 year olds are first-time breeders. To make an immediate distinction between auklets that have previously bred (adults) from ones that have not (sub-adults) the length of the gular pouch makes an useful criterion (Manuwal 1978). This specialized structure is an adaptation for transporting food long distances to the nest site and is present in all plankton-feeding auklets (Bedard 1969). Fledging Cassin's Auklets have no gular pouch, but the pouch begins to develop when the bird breeds for the first time, usually at 3 years of age. The pouch reaches a maximum

distended length of about 125 mm when they are feeding their nestlings, but regresses to about 65 mm after the breeding cycle (Manuwal 1978). If gular measurements are taken during the incubation stage it may be possible to determine if the breeding birds in question are first time breeders or not.

To measure the gular pouch a thin glass rod will be inserted into the pouch below the tongue. The rod will be coated with vaseline so it doesn't damage the pouch. The rod will be inserted gently until resistance is felt. The rod will then be pinched at the tip of the bill and then the distance between my fingers and the end of the rod will be measured (Manuwal pers com.)

Programed mass loss

'Condition' indices based on size-adjusted body mass have been used commonly in many avian studies, but this index may not be a true measure of the condition of the bird, ie. some alcids lose mass to facilitate a programmed response to increased flight demands during incubation and chick rearing (Gaston and Jones 1989 Ancient Murrelets; Croll et al. 1991 Thick-Billed Murres; Jones 1994 Least Auklets; Knechtel 1995 unpublished Cassin's Auklets). Therefore, a bird with a large size-adjusted body mass may not be considered a 'high quality' bird. The criterion for mass loss to be adaptive and not stress-related is for the loss in mass to be stepwise and abrupt as apposed to a gradual and continuous throughout the breeding season. Adaptive mass loss occurs in Triangle Cassin's Auklets usually at the beginning of incubation when the brood patch is beginning to refeather. What are the fitness consequences of mass loss? Are individuals which fledge larger chicks the ones which lose more

mass at the start of incubation? To what extent is mass loss a 'quality indicator'? Is mass loss an adaptation to molt rather than to the increased flight demands on the parents during chick rearing?

During the 1994 & 1995 night banding of Cassin's Auklets many birds were captured and weighed on multiple occasions, which allowed for the creation of a mass history through the two breeding seasons for different individuals. This history will allow me to look at the point during the breeding season where the adaptive step-wise mass loss took place. By monitoring burrows above the capture nets, it will be possible to follow the reproductive effort of marked individuals by weighing and measuring these individuals and their chicks, and recapturing the adults during the nocturnal net capture efforts. Multiple recaptures of individuals with previous multiple recapture histories will allow for comparison of individual mass histories over three breeding seasons.

Molt

Molt, which usually is temporally independent of breeding is an energetically demanding process. Thus species which overlap molt and breeding form something of a paradox (Foster 1975). The auklets (*Aethia* spp., *Cyclorhynchus psittacula*, *Ptychoramphus aleuticus*), molt their primaries over an extended period that overlaps with breeding (Payne 1965, Bedard and Sealy 1984). The wing molt of Cassin's Auklets involves the gradual loss and replacement of primaries a few at a time, from the innermost outward, rather than the simultaneous loss and replacement that occurs in the larger alcid. This asynchronous or gradual body, remix and rectrix molt allows Cassin's Auklet to fly throughout the year. To better assess

the quality of the Cassin's Auklet parents the timing of primary & secondary feather molt will be monitored.

Payne (1965) showed that the progress and rate of molt are slower in Cassin's Auklets that have expended the most energy in breeding, in other words auklets feeding their young are farther behind in their molt than auklets incubating their eggs. The 1994 Triangle Island night-banding data collected on the molt of primaries in Cassin's Auklets shows that the first breeding bird caught with a molted primary occurred on May 18th, one day before the mean hatch date for that year. Emslie et al. (1990) reported that in Cassin's Auklets, the energy demands of breeding and molt are independently unknown, but they are great enough to cause a slowing or suspension of molt. This study also indicated that males molt earlier and more slowly than females. During chick rearing, both adults spend the day at sea and return to the colony at night to feed food stored in the gular pouch to the chick (Speich and Manuwal 1974). The absence of one or more primaries on each wing would cause increased wing loading, especially with extra food in the gular pouch (Emslie et al. 1990). What is the relationship of molt and wing-loading?

During chick-rearing, when energy demands are the greatest, Cassin's Auklet parents lose mass and may continue an asynchronuous molt of their remiges, although molt stops completely in some adults that are feeding their young. The mass loss is considered adaptive due to the increased flight demand to provision their chicks. Molting at this time is thought to be adaptive since Cassin's Auklet plumage is extremely worn from months of life in the

burrows (Payne 1965). What is the relationship between molt and mass loss? Does the degree of mass loss affect the degree and timing of molt?

Cassin's Auklets are small birds with high energy demands, especially during the chick-rearing stage. For them to forage profitably on prey that are orders of magnitude smaller than themselves, it is probable that the prey must be concentrated (Brodie et al. 1978; Bradstreet and Brown 1978). Molt-breeding overlap is observed in arctic/sub-arctic species where resources are abundant for only a brief period (Johnston 1961, Hunter 1984). This appears to be the case with Cassin's Auklets, who feed on micronekton and macroplankton which increases in availability, becoming concentrated higher in the water column and closer to the breeding colony (Hunt et al. 1992) during its relatively long (when compared with other alcids) chick-rearing stage.

Molt-breeding overlap can occur only if energy and nutrients are adequate for both activities to occur simultaneously (Zaias and Breitwisch 1990). Through multiple capturing of individual parents in which their stage of breeding is known, I will be able to correlate the stage in the breeding cycle an individual is in with the extent of its molt using a method developed by Bensch and Grahn (1993) to estimate individual speed of molt. Since Cassin's Auklets can alter timing and rate of molt in relation to breeding effort, apparently as a means to balance the energy demands of both, (Emslie et al. 1990) auklets which arrest their rate of molt early in the breeding season are expending more energy than birds which continue molting to a later stage in the breeding cycle. By looking at the variation in

timing and rate of molt of parents of known chicks I will be able to better understand the relationship between molt of the parents and the growth of their chick. The nesting success of individuals with or without molt overlap will be compared by relating the growth rates and fledging weights of young reared by molting and non-molting parents.

Wing Loading

Wing loading, a fundamental component of avian wing design, affects speed, maneuverability, and energy expenditure during flight (Rayner 1988, Pennycuik 1989, Norberg 1990). Within species, wing loading can exhibit age and sex specific variation (Blem 1975, Mueller et al. 1981). Furthermore, widespread intraspecific variation in wing length (Alatalo et al. 1984) and wing shape (Hedenstrom and Pettersson 1986, Mulvihill and Chander 1990) suggests that the variation in wing loading within species is common. This raises the possibility of ecologically significant covariation of aerodynamically important traits such as wing loading with foraging behaviour, susceptibility to predation (Chandler and Mulvihill 1992) and in Cassin's Auklets the ability to nightly fly long distances between their foraging area and their burrow to feed their chick. Cassin's Auklets use their wings to swim under-water, where large wings can be a handicap because of their friction with the water. As a consequence, Cassin's Auklets have small, thin, but muscular wings which causes heavy wing-loading and poor flying ability. Emslie et al. (1990) indicated that males initiate primary molt earlier than females. This may be because males have lower wing-loading than the females. By characterizing an individual's relationship between wing loading, molt, body mass

and breeding success I will be better able to assess an individual's 'quality'.

By tracing the right wing of each parent on graph paper when they are pulled from their burrow late in incubation and later determining the area of the wing using a planimeter I will be able to determine the wing-loading for individuals (Hedenstrom and Moller 1992). By capturing, weighing and scoring the primary molt on these individuals on multiple occasions I will be able to assess how an individual's wing-loading changes through the breeding season.

Blood parameters as measures of quality

White blood cell count

White blood cells or leukocytes are part of the immune system and the number and proportions of different types of leucocytes reflect the health status of the individual. They respond quickly to a variety of stimuli, including stress, disease and allergic reactions (Fox and Solomon 1981; Bubenik and Brownlee 1987). The most frequently occurring type of leukocyte in most avian species is the lymphocyte; the second most common being the heterophil (Sturkie 1986); but some bird species have more heterophils than lymphocytes (DeVilliers 1938; Hawkey et al. 1985). Three other types (eosinophils, basophils, monocytes) occur in only small numbers (Sturkie 1986). The typical response to infectious diseases in birds is an increase in the total leucocyte count, mainly caused by an increase in number of heterophils and lymphocytes (Wilson and Wilson 1978; Davis 1981; Hawkey et al. 1983, 1985; Averbek 1992). Sometimes the response in birds will be an increase in the number of eosinophils (Wilson and Wilson 1978; Fox and Solomon 1981;

Powell 1987; Dieterlen-Lievre 1988). By collecting blood smears from individual breeding birds (Bennett 1970) (a quick and noninvasive method, since a femoral artery or vein (below the knee) only needs to be pricked and a small amount of blood collected) then air drying the smears, after which they should be fixed in absolute methanol for 5 min. and then stained with Giemsa pH7.2 for 20 min. (Dufva and Allander 1995). I will be able to count the number and types of leukocytes present within a given area of a slide on return from the field.

For a small percentage of the birds bled for leucocytes, blood will be collected to measure haematocrit values (the volume of tightly packed red cells in a blood sample) using a portable microspin. By counting the number of leucocytes per 10000 red blood cells and multiplying this value by the haematocrit, I can obtain the concentration of the different leucocyte types circulating in the blood (Dufva and Allander 1995).

Blood smears will be collected from individual parents during late incubation with an effort being made to try to collect blood at the same point in incubation and at the same time of day. A diel periodicity of leucocyte abundance has been observed in pigeons, caused by an absolute and relative increase of heterophils in the afternoon (Shaw 1933). Blood smears will be collected from the same individuals during the chick-rearing stage by catching them in nets during night banding; allowing for a comparison of numbers and types of white blood cells in individuals at different points during the breeding cycle. This comparison of an individual's white blood cell types and numbers at different stages of breeding will

possibly give me an indication of the amount of stress a parent incurs during the breeding cycle.

There are problems in interpreting what low or high leucocyte levels in the blood means. The number of leucocytes in the blood is a function of infection, the ability to fight the the infection and the numbers remaining after the immune system has interacted with the pathogens. Therefore, high leucocyte levels may reflect low immunocompetence, high immunocompetence or both.

Blood parasites

Parasites have the potential effects on the survival and fitness of hosts. Chronic parasitic infection may cause nutritional stress and mortality by the foraging ability of the infected animal. In contrast, parasitologists suggest that most parasitic infections in vertebrates are relatively benign.

Colonial seabirds seem relatively immune to blood parasites, such as haematozoa because of a lack of vectors in their nesting habitat. Greiner et al. (1975) recorded no haematozoa in four species of alcid from the northern temperate zone, but blood smears collected for leukocyte counts will be examined for parasites.

Ticks

Morbey (1995) demonstrated that the level of tick (*Ixodes uriae*) abundance found on developing Cassin's Auklet chicks had an effect on their wing growth rate and fledging age. Tick abundance on developing chicks will again be monitored. Ticks can cause holes to form in the webs of young Cassin's Auklet chicks which will persist throughout its life. The webs of parents who's burrows I'm monitoring will be scored for holes from zero to three; zero being no

holes and three being many large holes. It is possible that holes in the webs of adults can affect their foraging ability or since their growth was affected during their development, their parental quality might be less than birds who have no ticks during their nestling stage.

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Protocol

1. **Access of Burrows** Between March 20 and March 26, 400+ burrows (8 groups of 50) will be grubbed to allow easy access to the nest chamber. By grubbing burrows before the birds lay a minimum of disturbance will be caused. Each access hole will be capped with a piece of cedar shingle, while each burrow will be assigned its own number with corresponding wire flag. The location and configuration of each burrow will be mapped out in a field note book. Safe places to step on the breeding slope will be marked with flagging tape and wire to minimize the caving in of burrows.

2. **Determination of Mass Before Lay** Night banding will be carried out at the West Bay catching site for 2 to 4 nights before laying begins to determine the mass of as many individuals as possible before laying begins.

3. **Determination of Lay Date** Starting on March 26, half the burrows will be checked on alternating days. Burrows will be checked every other day until an egg has been laid.

4. **Catch Individual Parents to Measure Condition** Roughly 25 to 30 days after lay date parents will be removed from their burrows (Adults have a 24 hour incubation shifts) trying to control for lay date. Eggs will be measured (length, width and mass) and marked with corresponding burrow number. Birds will be banded with steel F&W bands. Their web damage and eye colour will be scored. The right wing will be traced (to determine wing loading) and then photographed to score retraction raggedness. Culmen, bill-depth, tarsus, wing chord and mass will be measured. The depth of the gular pouch will be determined with a thin glass rod (to determine previous breeding status). A small amount of blood will be collected from a femoral artery or vein for a blood smear.

5. **Determination of Hatch Date** 35 days after lay, burrows will be checked for hatch and every other day after that until hatch.

6. **Cross Fostering Experiment** Controlling for hatch date, 150 chicks will be switched between burrows 5 to 7 days after hatch (after brooding). Large chicks with large parents will be switched with small chicks with small parents.

7. Chick Growth Data Chicks will be weighed and their wing-chord will be measured at hatch. At 5, 25, 35, 40, and every two days after until fledge, chicks will have their tarsus, wing-chord, culmen, bill-depth and mass measured. A small amount of blood will be collected at 25 days of age to determine the sex of the chick (molecular DNA technique R. Griffiths 1992).

8. Recapture of Adults Trying to control for hatch date, adults will be recaptured at their burrows 3 to 4 times during the chick-provisioning period. A PVC pipe burrow trap with a closing door will be placed in the burrow entrance. A door will be tripped by the auklet as it walks into the burrow to feed its chick, trapping the adult in its burrow but still allowing it to feed its chick. Molt will be scored, mass measured and blood will be collected. Some burrows will be monitored above the nocturnal catching nets allowing them to recaptured on multiple occasions.

9. Measurement Error Cassin's Auklet carcasses will be collected throughout the field season and frozen for analysis on return from the field.