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COLONIALITY OF BROWN BOOBY (*SULA LEUCOGASTER)* IN GORGONA NATIONAL NATURAL PARK, EASTERN TROPICAL PACIFIC

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Resumen. – Colonialidad del Piquero Café (*Sula leucogaster*) en el Parque Nacional Natural Gorgona, Pacífico Oriental Tropical. – Se han planteado muchas hipótesis para explicar cómo la cría colonial puede beneficiar a los individuos que la practican, pero existe débil soporte para estas y ninguna parece ser una explicación generalizable a todas las colonias. De octubre de 2002 a octubre de 2003 se intentó precisar cuál de las hipótesis para explicar la colonialidad (centro-periferia, centro-satélite o al azar) se ajustaba más al piquero café en Isla Gorgona (Colombia). Se encontró una población reproductiva de 300 individuos criando asincrónicamente. Los nidos presentaron un patrón de disposición espacial agregado con distancia promedio al nido más próximo de 1,6 m. El éxito de eclosión y el éxito reproductivo anual fueron de 28,2% y 17,3% respectivamente. El modelo centro–periferia, donde la variación en supervivencia en una colonia se origina porque los individuos centrales son menos accesibles a depredadores, son de mejor condición física y tienen mayor éxito reproductivo, no se ajustó a las colonias del piquero café en Gorgona. La disposición espacial de la calidad de pareja mostró una clara autocorrelación espacial negativa en el primer intervalo de distancias (0 a 1,5 m), lo cual indica que hubo atracción de parejas de alta calidad sobre parejas de baja calidad, ajustándose esta predicción al modelo centro–satélite y a un patrón de disposición de nidos agrupado. Este modelo, que predice la atracción de individuos de baja calidad alrededor de los mejores sitios de crianza ya ocupados por individuos de alta calidad, fue consistente durante todo el año. En consecuencia, la hipótesis de reducción de la depredación y el modelo centro–periferia derivado de la misma no son generalizables a todas las colonias de aves marinas.

Abstract. – Many hypotheses have been considered to explain how colonial breeding can benefit individuals who practice it; however, these hypotheses are supported by weak evidence. On Gorgona island, during October 2002 through October 2003, Brown Booby (*Sula leucogaster*) nest sites were physically characterized and periodically visited in order to describe the reproductive cycle and explain coloniality hypotheses and nest site position (center-periphery, center-satellite or at random). We found a reproductive population of 300 individuals breeding asynchronously. Nest sites followed an aggregated pattern with an average nearest neighbor distance of 1.6 m. Hatching success of population during the whole year was 28.2%, and reproductive success 17.3%. This success was closely related to nest site position in the colonies. The center-periphery model, which suggests that variation in survival is generated by the fact that central individuals are less accessible to predators and have better physical conditions and higher reproductive success than periphery individuals, was not supported by Brown Booby colonies in Gorgona. The spatial disposition of quality of pairs shows a negative autocorrelation in the first distance interval (0 to 1.5 m), which

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indicates that there was an attraction of pairs of low quality towards pairs of high quality. This suggests that center–satellite patterns and aggregated patterns were predominant. The central-satellite model which predicts the attraction of individuals of low quality towards the best breeding places already occupied by individuals of high quality was consistently observed throughout the year. In conclusion, the center–periphery pattern derived from the predation-dilution hypotheses does not fit all the colonies of marine birds as proposed. *Accepted 24 June 2008.*

Key words: Brown Booby, *Sula leucogaster*, coloniality, central-periphery, central-satellite, nest site, predation, reproductive success.

INTRODUCTION

Colonial breeding happens when the individuals of one species group themselves densely to breed in territories which do not contain other resources than the nesting sites. The costs identified for the evolution of coloniality are: increased mortality, transmission of parasites, mating outside pairs, infanticide, intraspecific competition for food, and cannibalism. Many hypotheses have been established to explain how colonial breeding can benefit individuals who practice it. However, these hypotheses are supported by weak evidence (Danchin & Wagner 1997).

The center-periphery model suggests that variation in survival is generated by the fact that central individuals are less accessible to predators and have better physical conditions and higher reproductive success than periphery individuals (Coulson 1968, Vine 1971). Protection and defense of nesting site against predators by individual dilution within the group and collective harassment of attackers are traditionally assumed to be important forces in the evolution of the coloniality (Lack 1968, Goetmark & Andersson 1984, Siegel-Causey & Kharitonov 1990). When not guarding against predators, members can spend their time in other activities (Terhune & Brilliant 1996) such as foraging. The great tendency of seabirds to breed in colonies suggests that aggregation is not only an adaptation for defense against predators, because actually this behavior results in more vulnerability (Clode 1993). The center-periphery hypothesis applies to nest site disposition of many seabirds colonies (Wittenberger & Hunt 1985, Furness & Monaghan 1987, Kharitonov & Siegel Causey 1988), but there are several examples where empirical results do not accurately fit this hypothesis; see Ryder & Ryder (1981) and Pugesek & Diem (1983) in the Ring-billed Gull (*Larus delawarensis*), Scolaro *et al.* (1996) in South American Tern (*Sterna hirundinacea*) and, Shaw (1985) in Imperial Shag (*Phalacrocorax atriceps*). The influence of predation on the disposition of breeding individuals in colonies is therefore still unclear (Danchin & Wagner 1997).

The commodity selection hypothesis assumes that nesting aggregation may be a byproduct of many individuals selecting commodities for breeding, such as habitat and mates (Wagner *et al.* 2000). Three types of conspecifics signals can influence the decision of an animal to choose or leave a breeding site: the presence of other individuals of its species, the reproductive success (RS) of conspecifics, and the characteristics of potential partners (Danchin & Wagner 1997). The center-satellite disposition model may appear in species which are attracted to nest near the best sites to enhance the chances of extra-pair matings, or to acquire better sites or pairs in the next season. The model describes the spatial association of pairs of low quality around a pair of high quality; it has been demonstrated that the

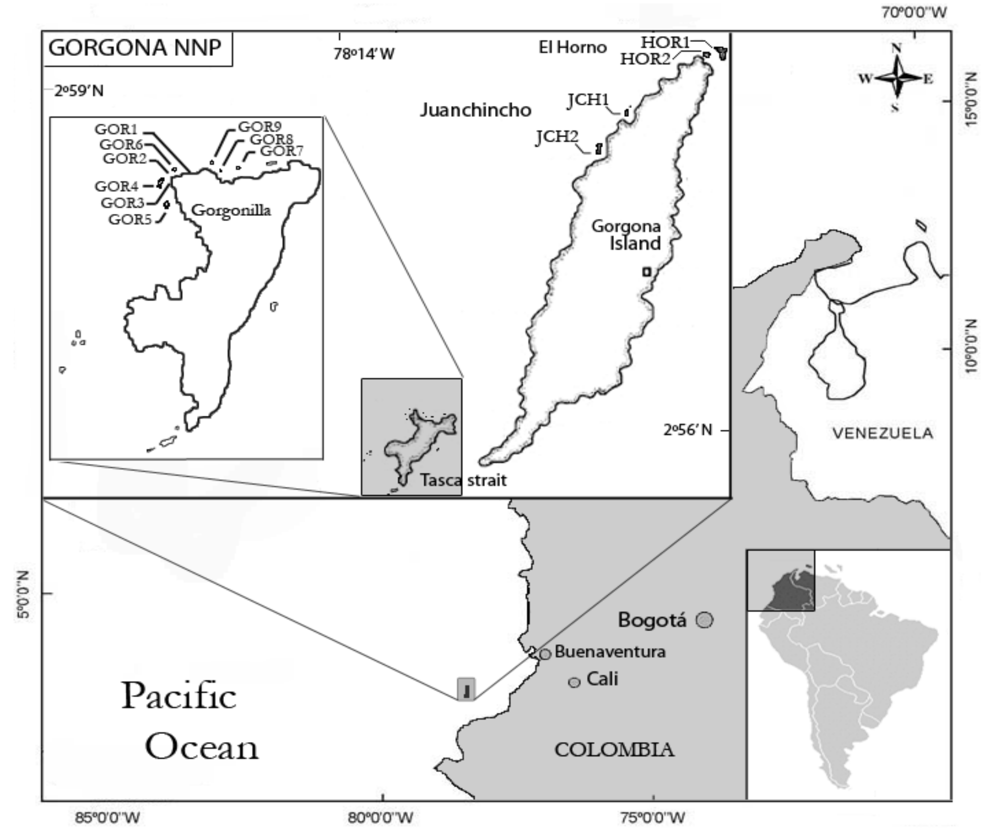


FIG. 1. Spatial disposition of Brown Booby colonies in Gorgona NNP. The zones are Gorgonilla (GOR), Juanchincho (JCH) and El Horno (HOR). Each colony is identified by alphanumeric code, three letters corresponding to zone and number.

spatial disposition of nests in reproductive colonies of European Shag (*Phalacrocorax aristotelis*) does not fit the center-periphery model, but rather adjusts to either the center-satellite model or alternative spatial dispositions (Velando & Freire 2001).

This study has tested center-periphery and center-satellite models in the Brown Booby (*Sula leucogaster etesiaca)* colonies in Gorgona National Natural Park (NNP), Eastern Tropical Pacific (ETP). We used reproductive ecology observations and analysis methods similar to those proposed by Velando & Freire (2001).

METHODS

This study was conducted in Gorgona NNP. Gorgona is the principal island, some 27 km from the Colombian Pacific coast (2°56’N, 78°12’W). Nearly the North coast are Horno (HOR) and Juanchincho rocks (JCH) in the NW. In the SW is Gorgonilla Island (GOR), separated from the coast by the 700 m Tasca strait. Around GOR there are many cays and rocks. The mean annual temperature is 27°C, the relative humidity is 88–95%, and the mean annual precipitation is 6,694 mm, September and October being the rainiest

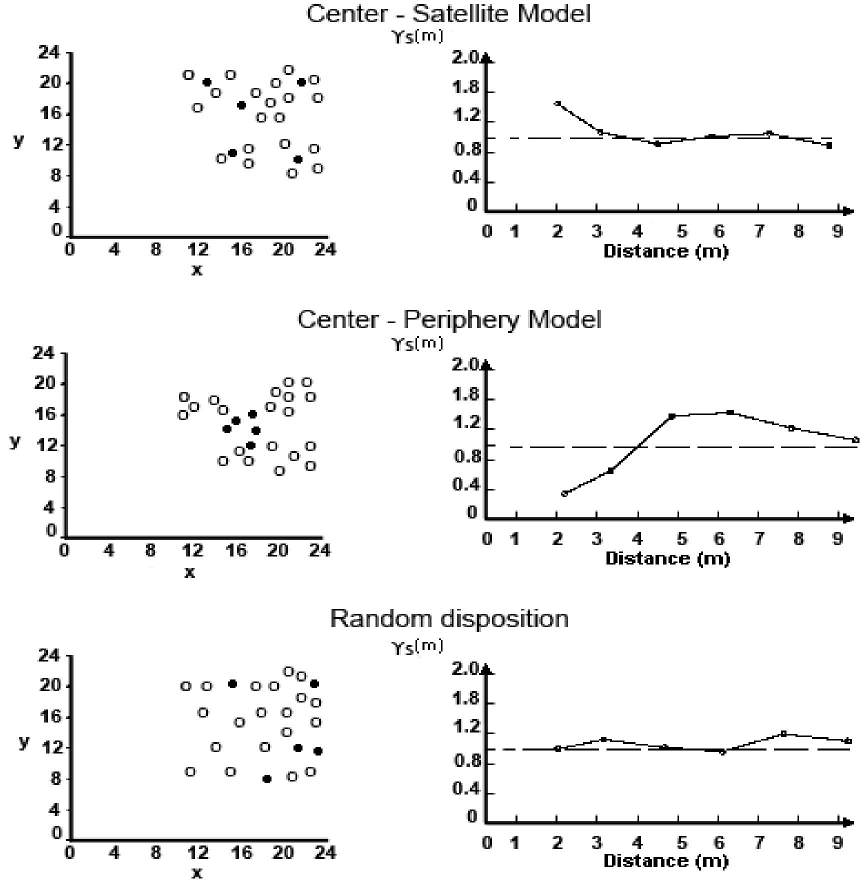


FIG. 2. Theoretical disposition of pair quality identified as reproductive success residuals for three nest disposition models. The disposition of reproductive success residuals is on the left side. The values in each axis are meters, the filled circles are positive residuals (high quality of pair), empty circles are negative residuals (low quality of pair). The standardized variograms for each model are on the right side. The pointed line is the standardized total variance, yS(m) is the standardized variance. High values of semivariance means negative autocorrelation and low values positive correlation.

months, while February and March are less rainy. There is no dry season. The superficial temperature of the water ranges between 27.0 and 28.5°C.

In October 2002, we confirmed the breeding occurrence of *S. l. etesiaca* in Gorgona NNP, subspecies described by Thayers & Bangs (1905) and with distribution between western Panamá and northern Ecuador, including Colombian waters. *S. l. etesiaca* was the only subspecies of Brown Booby nesting in the Gorgona NNP. We recorded eggs, chicks and fledges and backcalculated the beginning of breeding season in August. We found nine colonies in Gorgonilla (GOR1 to GOR9), two in Horno (HOR1 and HOR2), and two in Juanchincho (JCH1 and JCH2) (Fig. 1).

TABLE 1. Actual status of Brown Booby breeding populations in the Pacific Ocean.

Zones	Locations	Years	Estimated No. of nesting pairs	Sources
Eastern Tropical Pacific	Gorgona NNP	2003	150	Present study
Eastern Pacific	San Pedro Martir Island	1994	74000	Tershy *et al.*, unpubl. data, Tershy & Breese 1997
Eastern Pacific	Clipperton Island	2003	12500	Pitman *et al.* 2005
Eastern Tropical Pacific	Cabo Blanco Island	1996	1194	Chaves-Campos & Torres 2002
Central Pacific	Lehua Islet (Hawaii)	2003	1042	VanderWerf *et al.* 2007
Central Pacific	Johnston Atoll	2000	550	Beadell et al. 2003
Eastern Pacific	Isla Larga	2001	550	Rebón-Gallardo 2000
Eastern Pacific	San Benedicto Island	2000	300	Pitman & Ballance 2002

We visited each colony every 15 days, from October 2002 to October 2003. We mapped nest sites with X-Y coordinates. The X-axis corresponded to a horizontal line parallel to the coast. Distance between each nest site and others nest sites in the same zone were recorded. We analyzed the spatial disposition pattern with average nearest neighbor distance using analysis developed by Clark & Evans (1954), and modificated by Donnelly (1978). This modification corrected the absence of boundaries for the study area.

For each nest site we considered quantitative physical parameters: height (m), mean inclination (degrees), percentage of herbaceous cover, number of bordering walls (0–3) and width of platform (m). Also we considered qualitative physical parameters: type of land (top, cliff or platform), direction of inclination (null, towards the rock or the sea), roof presence/absence, cracks presence/absence, drainage type (good or dry, bad or floodable terrain). The reproductive success (RS) of each pair was assessed as positive if at the end of breeding season a fledged chick had left the nest. The nest sites physical quality index (NPQI) of the Brown Booby (R^2 Nagelkerke $= 0.486$, $\chi^2 = 33.961$, df $= 17$, $P = 0.0085$) relates the logistic binary regression of RS between October 2002 and July 2003 with all evaluated physical parameters (Ospina-Alvarez 2004). The residuals of this regression express the Pair Quality Index (PQI).

We used logistic multinomial regressions to evaluate the relation of accumulated reproductive success per nest site in JCH2. The accumulated RS is defined as the sum of the RS's from August to January and March to July with the physical parameters of nest site. Using residuals of this regression we obtained a PQI corresponding to the whole year. Two simulations of nests disposition models were made to visualize statistical characteristics of their spatial structure and to compare them with observed PQI's. We also simulated a random disposition model. The models were set up with 25 nest sites and an area similar to that of the JCH2 colony. The successful sites received a qualification of two, and unsuccessful sites a qualification of one. We used similar physical parameters for 25 nest sites (Index of similar physical quality), and assumed RS of 20% (Fig. 2). We used the same techniques of geostatistical analyses as used by Velando & Freire (2001): both theoretical and experimental models represent the semivariance between pairs of points (nest sites) separated by a lag (distance) m. The distance intervals

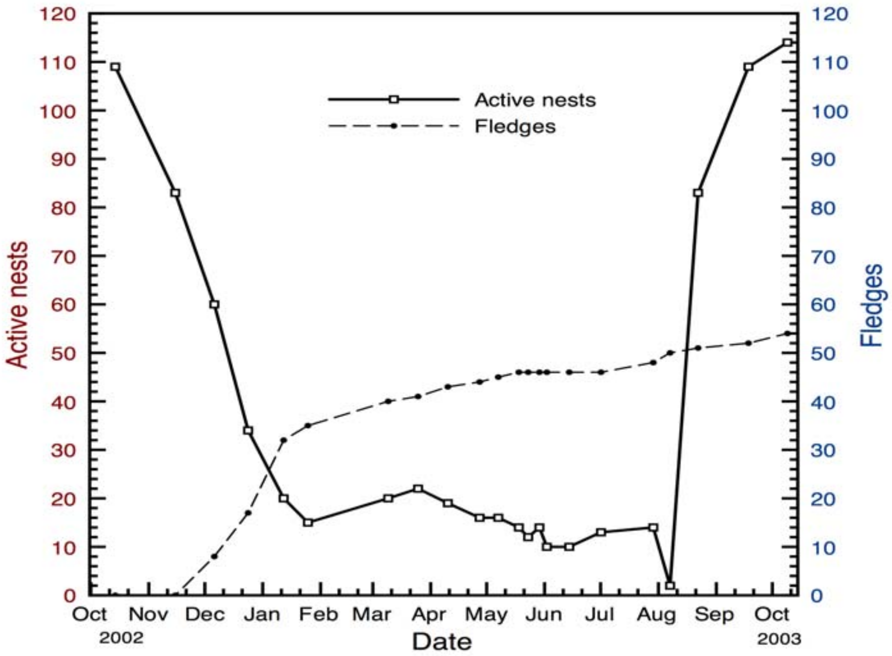


FIG. 3. Number of Brown Booby active nest (eggs or chicks presence) in Gorgona NNP and accumulative reproductive success indicated as number of fledges from October 2002 to October 2003.

were placed at 1.5 m. Semivariance was standardized by dividing it by the total variance of all the points. Variograms and correlograms were obtained with software VARIOWIN version 2.1 (Pannatier 1996). Spatial autocorrelation of pair quality in the JCH2 colony was statistically tested by the coefficient of product-moment correlation in the first interval. Graphical characteristics of the models were compared with graphs obtained from the spatial disposition of Brown Booby nest in the JCH2 colony and the PQI. In random spatial models, the distribution of pair quality is not assumed. The semivariance was standardized by dividing it by the total variance of all points. The standardized semivariance, measured like RS in a homogenous habitat, has a value near 1.0 ± 0.2, while the spatial autocorrelation of RS residuals to short distances does not exist (initial interval). In the center-periphery model, where the birds of high quality tend to occupy a central position in the colony, surrounded by birds of low quality, the standardized semivariance has low values at short distance and increases when the distance is greater. This model predicts a positive spatial autocorrelation relative to the residual in the initial interval. In a model center-satellite where there is an attraction of birds of low quality to nest near birds of high quality at short distances, the standardized semivariance is much higher than 1 and diminishes quickly when distance increases (Velando & Freire 2001).

RESULTS

Brown Boobies in Gorgona NNP were

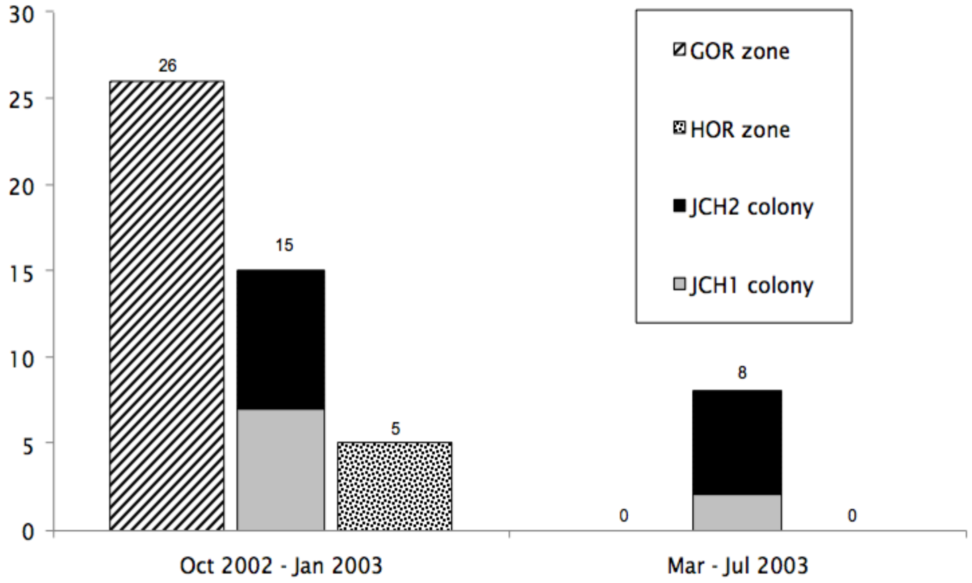


FIG. 4. Number of Brown Booby fledges in GOR, HOR and JCH zones in two reproductive seasons. During March–July 2003, Brown Boobies nested only in JCH zone (JCH1 and JCH2 colonies).

reproductively active during the whole year (Fig. 3). Greater activity occurred from October 2002 to January 2003 (132 pairs). Between March and July of 2003, 34 pairs nested, 27.4% of preceding reproductive peak. Among the three zones, GOR was more productive with 26 chicks fledged (Fig. 4), followed by JCH with 15, and HOR with 5. However, it is important to consider that GOR had 9 colonies, whereas JCH and HOR had 2 colonies each. The most productive colonies were JCH2 (8 chicks fledged) and JCH1 (7 chicks fledged). During October 2002 – October 2003 all nest sites were observed periodically from laying to recruitment (when fledged chick had left the nest), abandonment of eggs or chick's death.

From March to July 2003, 34 pairs nested in JCH zones (27.42% of pairs nesting last season). This was not observed in GOR and HOR. During this period, the JCH2 colony was more productive than JCH1 and fledged chicks were observed in October. During the study year, GOR was the most productive zone, and JCH2 the most productive colony (Fig. 4).

The Brown Booby breeding population estimated in Gorgona NNP was 150 pairs, small if compared to other breeding colonies of the species in the Pacific Ocean (table 1), or the whole world (Nelson 1978). The accumulated RS of Brown Boobies between October 2002 and October 2003 was 17.3%, corresponding to 54 recruits from 312 nest sites (table 2).

In Gorgona NNP, the Brown Booby nest sites followed an aggregated pattern between October 2002 and January 2003 ($P < 0.05$). In the breeding colonies, the mean density was 1 nest for each 26.9 m^2 and average nearest neighbor distance was 1.6 ± 0.8 m, (0.5 m minimum and 4.2 m maximum). This index does not allow other prediction to be made.

Because JCH2 was the largest colony with

TABLE 2. Reproductive success of Brown Booby in Gorgona NNP during October 2002 through October 2003. Clutch period 2 Oct. 2002 – 3 Oct. 2003 include total nest of two breeding seasons. The number of initial eggs was unknown for some nests at the beginning of the study.

Clutch period	No. of nest sites	No. of eggs laid	No. of eggs hatched	No. of young fledged	% eggs hatched	% of young fledged from Eggs	Hatching	Nests
Oct. 02 – Jan. 03	72	116	21	8	18.1	6.9	38.1	11.1
March 03 – Jul. 03	33	46	17	7	37.0	15.2	41.2	21.2
Oct. 02 – Oct. 03	312	?	?	54	?	?	?	17.31

24 pairs in the date of greater density, we chose JCH2 to make additional geostatistical tests. Experimental variograms were calculated for the August 2002–January 2003 and October 2002-October 2003 seasons. Experimental variograms were not elaborated for other zones of Gorgona NNP, because the nest sites numbers were relatively low, and it was not possible to obtain models with an acceptable number of pairs. JCH2 variograms compared with theoretical variograms (random, center-satellite and center-periphery) were used for analyzing the spatial disposition of pairs of high and low quality. In JCH2 we obtained a model relating RS's (PQI) residuals with nest sites dispositions for the August 2002–January 2003 reproductive season (Fig. 5). The semivariance standardized was 1.91 in the first interval, 1.09 in the second interval, and subsequently it fluctuated around 1. The average nearest neighbor distance was 1.43 ± 0.57 m. The characteristics of this model suggest for JCH2 a spatial association of pairs of low reproductive quality with pairs of high reproductive quality (P = –0.91 from the autocorrelation for interval 0 to 1.5 m).

Additionally, we elaborated a variogram relating the accumulative PQI (residuals of accumulative RS) with the disposition of the nesting sites in the whole year (Fig. 6). The semivariance standardized in the first interval was 1.55, soon decreased to 1.16, and continued fluctuating near 1.00 ± 0.20 in the other intervals. Average nearest neighbor distance was 1.48 ± 0.61 m. Again, the characteristics of this model suggest that Brown Booby colony in JCH2 demonstrates a spatial association low quality pairs with high quality pairs (P = –0.55 from the autocorrelation for interval 0 to 1.5 m).

DISCUSSION

The Brown Booby breeding population nesting in Gorgona NNP is small, but is the most important breeding territory for *S. l. etesiaca* in the world. The population of 150 pairs registered during this study exceeds the number of individuals in other regional localities (Naranjo *et al.* 2001).

Brown Boobies in Gorgona NNP breed asynchronously; on the same date, we recorded eggs, chicks in early or youthful stages, and fledged chicks. The calculated accumulative RS (17.3%) included more than 95% of all pairs breeding in this year, but this may change to year after year (Nelson 1978). In Gorgona, RS was similar to that of Ascension Island (18% and 26% in two consecutive seasons) and was considerably smaller than that of Kure (76.5% average 1964 to 1968) and Christmas Island (86%); results indicate local differences related to environmental conditions.

JCH1 and JCH2 were the most productive colonies in Gorgona NNP with 9 and 14

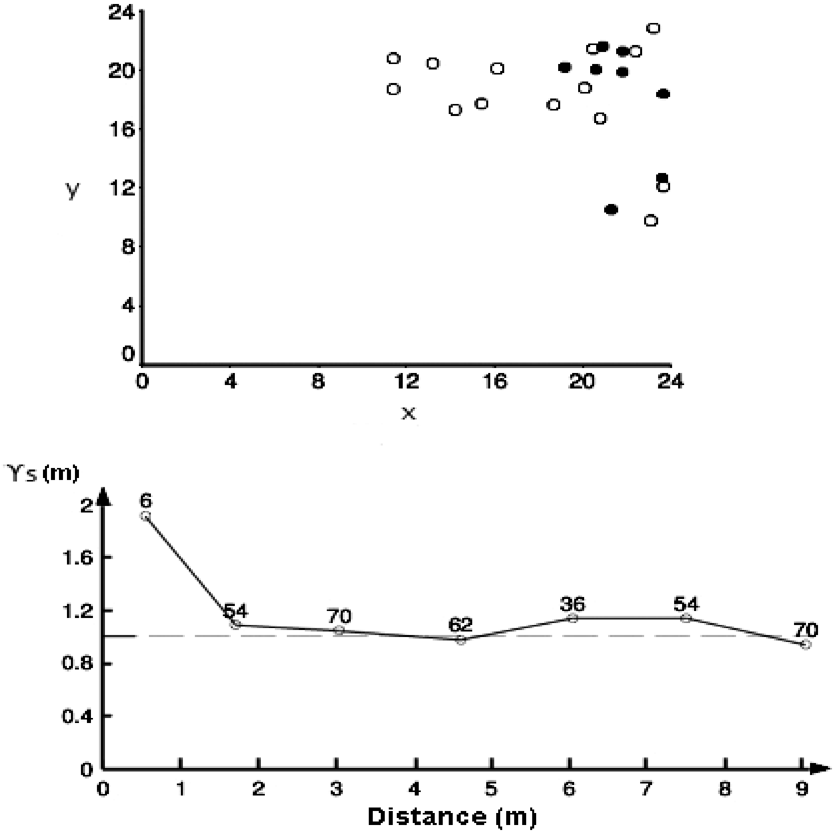
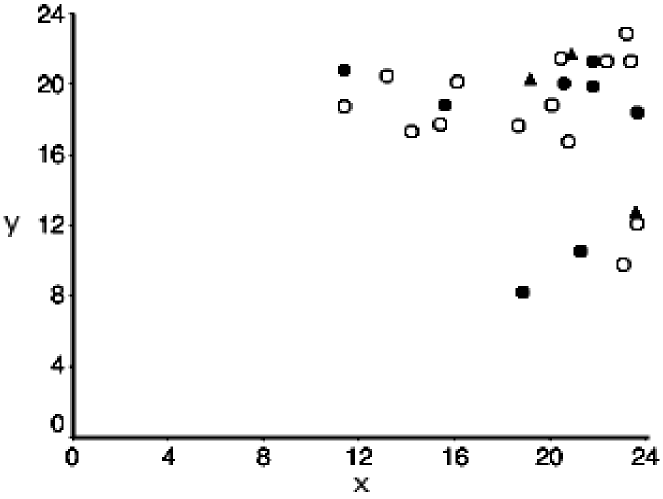


FIG. 5. Nests dispositions (above) and variograms using reproductive success residuals of the August 2002–March 2003 season in JCH2 colony. In both cases, the spatial disposition of reproductive success residuals is shown above. The values in each axis are meters, the filled circles represent positives residuals (high quality of pair), and empty circles represent negatives residuals (low quality of pairs). The standardized variogram is shown below. The pointed line indicates standardized total variance, yS(m) is the standardized variance. High values of the semivariance indicate a negative autocorrelation and low values a positive autocorrelation. The number of compared pairs is showed for each distance. The reproductive success was 36%.

recruits from 15 and 25 nest sites, respectively. In these colonies Brown Boobies practiced continuous breeding, indicating that the Juanchincho zone has special characteristics, such as better habitat quality or abundant food availability, unlike in GOR and HOR zones. Mellink (2001) suggested that reproductive colonies with pairs breeding during the whole year are in zones where the surrounding waters offer abundant food, like San Jorge Island (Baja California). Mellink related this to the prey variety found in the regurgitations and concluded that, in San Jorge, the Brown Booby incorporates, in its diet 30 species of fishes or more, including 15 benthic fishes, unlike what is found in colonies of other islands. If prey abundance is considered in all the zones, the RS can be attributed to



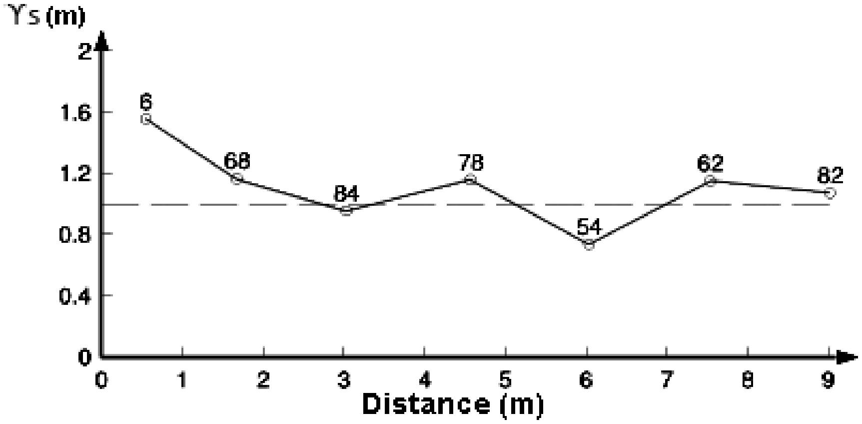


FIG. 6. Nest disposition (above) during October 2002 through October 2003 and variogram using accumulative RS residuals of Pearson (below) of JCH2 colony. In the disposition map, X axis is parallel to coastline and values for both axes are meters, the empty circles are nest sites without reproductive success, filled circles are nest sites where the reproductive success was of one fledged chick in one year of study, and filled triangles are nest sites where reproductive success was two fledged chicks in the same period. In the variogram, the pointed line indicate standardized total variance, yS(m) is the standardized variance. High values of the semivariance indicate a negative autocorrelation and low values a positive autocorrelation. The number of compared pairs is show for each distance. The successful sites with two fledges have a qualification of three (3), successful sites with one fledged have a qualification of two (2), and nest sites without success have a qualification of one (1). The reproductive success was 44%.

physical conditions of nest sites, high precipitation or other environmental conditions.

We discarded predation because we did not observe interspecific events of this type in Gorgona NNP populations, and we did not identify natural predators of importance. In accordance with Le Corre & Jouventin (1997) we discarded kleptoparasitism by Magnificent Frigatebird (*Fregata magnificens*). Le Corre & Jouventin determined in Red-footed Booby (*S. sula*) colony that less than 1% of population was loosing food due to Great Frigatebird (*F. minor*) and Lesser Frigatebird (*F. ariel*). Diverse adopted strategies were identified to evade aggressors, such as flying in big groups (> 50) or returning to colonies during periods of low light. In Gorgona, Brown Boobies form flocks with Blue-footed Booby (*S. nebouxii*), which can confer them hypothetical advantage.

Brown Booby breeding pairs in Gorgona established their nest sites on rocks or cays in an aggregated pattern disposition. This indicates interactions between individuals, or between the individuals and the habitat. According to Nelson (1978), nest density in Brown Booby colonies is highly variable; on Christmas Island, average nearest neighbor distance was 3.7 m with possibility of finding a nest every 13.4 m^2. The average nearest neighbor distance in Gorgona was about 1.5 m with inferior maximum values of 5 m for all colonies. These spatial conformations of nest sites must be related to great adaptability of Brown Boobies to diverse habitats, thus indicating that each area requires a special study.

If only the intrinsic factors are considered, aggregation could be a consequence of predominant reproductive strategies in the population; for example, pairs of low reproductive quality congregate around pairs of high quality. If additional extrinsic factors are considered, aggregation could be a consequence of resources pattern disposition, danger (defensive behavior), or taking advantage of resources patches of high quality, and depopulation of poor zones (Danchin & Wagner 1997). According to experimental variograms, the spatial disposition of pair quality in JCH2 shows a clear negative spatial autocorrelation in the first interval of distances (0 to 1.5 m). This negative spatial association of short distances of pair qualities as indicators of RS suggests there was attraction of low quality pairs toward high quality pairs, generating the center-satellite model and the nest aggregation pattern. The center-satellite model was observed in the JCH2 colony from August 2002 to January 2003 ($P = -0.91$) and from March to July 2003 ($P = -0.55$) seasons. The center-periphery model proposed by Coulson (1968) does not adjust to the JCH2 colony in Gorgona NNP during the whole year. The JCH2 colony has nesting sites with high physical quality and, possibly, abundant food, making JCH2 one of the most attractive sectors in the Gorgona NNP. This can explain why Brown Boobies breed in this colony during the whole year.

In Gorgona NNP, the high physical quality sites for Brown Booby nesting are completely occupied, but abundant sites of lower physical quality are equally occupied. This patchy environment generates a center-satellite pattern, because strong competition for the best nest sites exists, suggesting the commodity selection hypothesis under the study frame of conspecific attraction (Danchin & Wagner 1997). Seabirds which nest in homogenous habitats with low variability in physical quality index are often attracted to nest near others because breeding habitat quality depends only on the presence of conspecific pairs (Birkhead & Harris 1985) and, additionally, density can offer protection to predators; however, this benefit would be a conspecific attraction by-product and not a factor of aggregation.

In Gorgona all the conditions necessary to generate a nest disposition center-satellite pattern can be found: there is a patchy habitat, Brown Booby population is small, there are clear differences in physical quality between nesting sites, and there is an absence of natural predators. Therefore, the center-periphery model and reduction of predation hypothesis of Coulson (1968) are not applicable to all seabirds colonies. Velando & Freire (2001) reached this conclusion in their study of the European Shag. Results of this research confirm this conclusion in Brown Booby, a pelecaniform species living in a tropical region.

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