Natural Restoration of the Species-Area Relation for a Lizard After a Hurricane

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We document the decimation and recovery of the commonest lizard species, *Anolis sagrei*, on 66 islands in the Bahamas that were directly hit by Hurricane Floyd in September 1999. Before the hurricane, an island's area was a better predictor of the occurrence of *A. sagrei* than was its altitude. Immediately after, altitude was a better predictor: Apparently all lizards on islands lower than about 3 meters maximum elevation perished in the storm surge. After about 1 year, area again became the better predictor. By 19 months after the hurricane, *A. sagrei* populations occurred on 88% of the islands they formerly occupied. Recovery occurred via overwater colonization and propagation from eggs that survived inundation, mechanisms that were enhanced by larger island area. Thus, natural processes first destroyed and then quickly restored a highly regular species-area distribution.

The community species-area relation, describing the increase of species number with increasing area, is one of ecology's most pervasive regularities—even, perhaps, one of its few "laws" (*1–6*). This curve is itself composed of often quite regular occurrences for individual species: At the extremes, islands having or lacking a given species are entirely nonoverlapping in area, giving a steplike species-area relation for that species (*7*). A variety of causes for the species-area relation at both the community and individual species levels have been proposed (*1–6*). In the MacArthur-Wilson equilibrium model (*1*), for example, extinction rate is assumed to increase with decreasing population size, an assumption for which there is much evidence (*8–11*). Were population size less the smaller the area, individual species would tend not to occur on smaller islands, and fewer species would result there.

Other ways in which area might affect species occurrences can be more indirect. There is the possibility that larger areas might have greater maximum (or average) altitude. This may have two consequences. First, the greater the altitudinal range, the more kinds of habitats are likely to be found on the island, allowing more kinds of species to exist; many studies have explored this issue with correlation analysis, variously finding altitude, habitat diversity, or area to be most related to species number (*12–14*). Second, the higher the island, the more invulnerable are its populations to catastrophic inundations caused by natural events such as hurricanes and earthquakes. According to this line of reasoning, area is important because it is correlated with another variable, altitude, that is even more important. It would follow that were this correlated variable measured directly, the relation to species occurrences should be even more precise.

We have been studying the occurrences of lizard species on islands of the Bahamas for several decades. The turnover (the change in species occurrences via extinction and immigration) in the absence of major exterminating agents such as catastrophic storms is very low (*15*). Assuming a low immigration rate, one might expect the occurrences of lizards to be more strongly related to altitude than area; that is, to reflect the high-water mark of the major hurricanes that periodically devastate the Bahamas (*16*, *17*). However, we have found area rather than altitude to be a better predictor of the occurrence of lizard species, both over large regions (*6*) and at specific sites. An example is given in Fig. 1 (top left: prehurricane). For 66 small islands from a site off Great Abaco measuring about 7 by 2 km, the occurrence of the commonest lizard species, *Anolis sagrei*, showed a stronger relation to area than to altitude (*18*). The figure also shows that area and altitude in this archipelago are strongly correlated (Pearson $r = 0.85$; $P < 0.0001$). In unifactorial logistic regression, each of area and altitude is significant by itself. However, in stepwise logistic regression, area is entered first and altitude is omitted, explaining no additional significant variation in occurrence (*19*). Given the arguments about the directly exterminating effect of inundation during natural catastrophes, how could area be more important than altitude?

Nature began a demonstration of how area attains its importance on 14 September 1999, when Hurricane Floyd, a category IV hurricane with maximum sustained winds ~250 km per hour, passed directly over the archipelago shown in Fig. 1. We were able to reach the islands about 2 months later and survey them for lizards. Surprisingly, only very small lizards (that is, no adults or near adults) were found on a substantial number of islands (*20*). Such lizards by their size can be surmised to have hatched from eggs since the hurricane (*17*). Experiments now under way show that, indeed, lizard eggs (at least those ≤10 days old) can survive submersion in sea water for up to 6 hours, which is approximately the maximum duration of the storm surge according to locals, with no detectable ill effects. We infer that when an island is completely inundated during high water, eggs can weather the storm, even though all hatched lizards are drowned, washed away, or otherwise perish.

We found adult or nearly adult lizards, individuals that had not been killed or washed away, on 12 of the 66 islands 2 months after the hurricane. These 12 islands tended to be both higher and larger than those having no adult lizards, but the threshold of separation for altitude was visibly more precise than that for area (Fig. 2). Stepwise logistic regression confirmed this impression, with only altitude entering the model [although both variables again were significant in unifactorial regression (*21*)]. Islands with and without adult lizards overlapped in altitude over the range from 2.6 to 3.2 m, as compared to a range for all islands of 0.4 to 6.1 m. This rather precise threshold, about half a meter wide, which coincided with substantial reductions of leaf litter and topsoil, can be inferred to correspond to the height of the storm surge; that is, to the maximum rise in sea level resulting from the hurricane.

Seven months after the hurricane (April 2000: Fig. 1, top right), islands showed a less precise altitudinal threshold than 2 months after the hurricane (compare to Fig. 2) but also a less precise areal threshold than before the hurricane (compare to Fig. 1, top left). As for 2 months after the hurricane, stepwise logistic regression again selects altitude as the only significant variable, although both area and altitude are significant in unifactorial analyses (*21*). This state of affairs reverses 14 months after the hurricane (November 2000: Fig. 1, bottom left), when it is area, not altitude, that is solely selected by the regression. The latter situation persists at the final survey (April 2001: Fig. 1, bottom right), 19 months after the hurricane (*21*). Again in these analyses, both variables are significant in unifactorial regression. Hence, altitude loses its primacy over area rather quickly as time elapses after the hurricane.

For islands where *A. sagrei* was the only

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lizard species, lizard establishment was permanent: Once an island was found to have those lizards, it was never found without them. The only island having a second species of lizard, *Leiocephalus carinatus* (predatory on *A. sagrei*), was the only exception to the trend: Although a few *A. sagrei* were seen on that island after the hurricane, at the last census it had no *A. sagrei* and was the largest previously inhabited island by far to be in that state (Fig. 3, bottom right). Elsewhere (*17*), we showed that other islands of its area on which *L. carinatus* were artificially introduced mostly also lost *A. sagrei*. Although post-hurricane colonization and then extinction were thus generally not observed as part of the reconstitution of lizard-inhabited islands, unobserved colonization followed by unobserved extinction (or vice versa) is, of course, always possible during an interval between two surveys [for example, see (*22*)]. However, if in-and-out events were common, we should have detected more with our rather frequent censuses.

The reconstitution of islands having *A. sagrei* lizard populations before the hurricane is shown in Fig. 3. After ~2 months, we found adult or near-adult lizards on 12 of 49 islands; after 7 months, we found such lizards on 33 of 50 islands; after 14 months, we found such lizards on 43 of 50 islands. By the last survey, 19 months later, we found adult or near-adult lizards on 44 of the 50 islands; that is, 88% of the islands that had lizards before the hurricane were found to have them again. Note from Fig. 3 how the recovery of lizard occurrence proceeds down the altitude-area plot from larger to smaller values of both variables. Excluding the *L. carinatus* island, the five islands unoccupied by *A. sagrei* at the end of the study are five of the seven with the smallest area. In contrast, many reconstituted islands are quite low in altitude, broadly overlapping the altitudinal values for the unoccupied islands.

Lizard populations became reconstituted on an island by two mechanisms: overwater recolonization and multiplication from surviving eggs. The 21 cases of islands concluded to have acquired near-adult or adult lizards between the first and second censuses may be due to recolonization and/or repopulation via surviving eggs (hatchlings at the first census would have grown to near-adult or adult sizes by the second census). There is no way to be sure which mechanism was involved or whether both were involved; 2 months after the hurricane, we found hatchlings on 10 of those 21 islands that could have founded populations. Founders could have been supplemented by natural colonists. Further, the islands on which we saw no hatchlings still may have had them, because such islands can be quite large, so that one is then looking for needles in haystacks (see also caption of Fig. 2). Survival as eggs was doubtless a significant part of the reconstitution of lizard populations on islands (*17*). On the other hand, distributional gains between the second and third post-hurricane censuses and between the third and fourth censuses (10 islands and 2 islands, respectively) are most likely due to overwater recolonization. This is a rather large amount of species immigration when compared to the natural magnitude as estimated in a previous study at a different site (*15*), in which only one immigration of any lizard species was observed on 89 islands in 2 years, but of course a different and much larger set of islands was available after the hurricane than during "typical" times.

No evidence exists that the hurricane itself transported lizards: We found no island inhabited by lizards immediately (2 months) after the hurricane that was not inhabited before [but see (*18*)]. One island known not to have lizards immediately before the hurricane had lizards after it. This island was apparently colonized between 14 and 19 months after the hurricane; it was continuously uninhabited by lizards for at least 11 years before the hurricane struck. Its colonization exemplifies the low but finite natural turnover characterizing this system (*15*).

The rapid and fairly complete reconstitution of lizard occurrence found in this study is in some contrast to the only other such data in existence, those collected 3 years before in the wake of Hurricane Lili (*16*). On 19 October 1996, Lili passed directly over another of our study sites, a set of islands in the central Bahamas off Great Exuma, also terminating an experiment. Although of lower wind speed than Hurricane Floyd (the hurricane of the present study), Hurricane Lili generated a substantially higher storm surge, attaining about 5 m and largely devastating vegetation on exposed islands. All lizards perished, and thorough searches immediately after the hurricane as well as ~3 months later produced no hatchlings (or lizards of any kind) on any of the experimental islands. Of the five similarly sized islands at that site

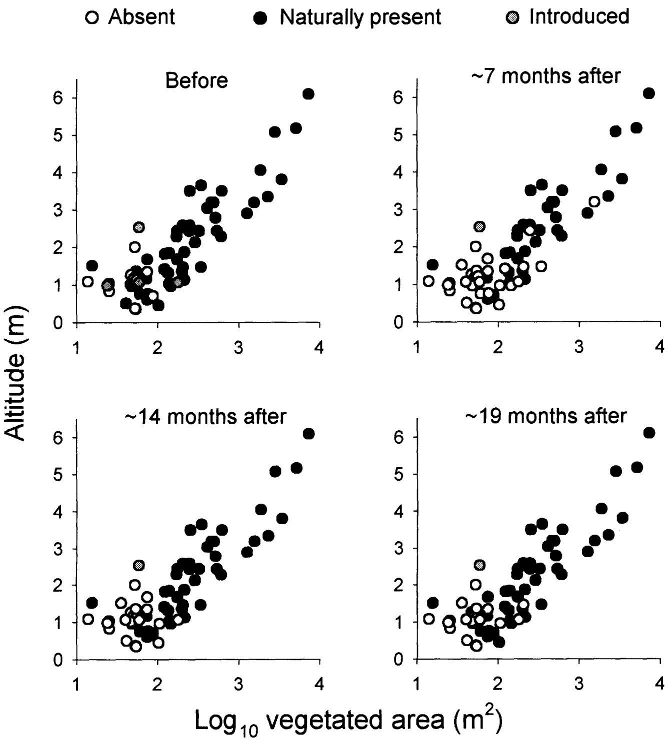

Fig. 1. Occurrence of *A. sagrei* in relation to island area and altitude. Each point represents a separate island in the archipelago. There is a very strong correlation between the two variables. "Absent" means the lizard was not found to occur on the island. "Naturally present" means the lizard was found on the island and had gotten there by natural means. "Introduced" means the lizard occurred on the island as a result of experimental introduction in either 1977 (*31*) or 1988 (*32*). Sample sizes are as follows: before the hurricane = 63 islands; ~7 months after = 66; ~14 months after = 66; and ~19 months after = 66.

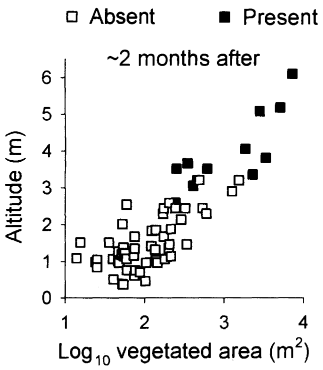

Fig. 2. Presence and absence of adult or near-adult *A. sagrei* lizards immediately after the hurricane (November 1999). There is a much sharper occurrence threshold for altitude than for area. All islands marked "present" had lizards that survived the hurricane's effects as hatched individuals. Islands marked "absent" had no lizards seen or had only very small, hatchling lizards seen: those that would have been in the egg stage (and thus not yet hatched) during the passage of the hurricane. Sample size = 65 islands.

known to have *A. sagrei* lizards naturally, lizards were found on only one after a 12-month interval, and lizards have been seen on three of the five up to the present, 4 years later. We suggest that the physical force of the storm surge, much greater at the Exuma site, was much more devastating to the egg stage there; indeed, the vegetation at the present (Abaco) site was much less reduced than at the Exuma site. Seasonal reproduction of anoles in the Bahamas (*23*), with activity tapering off in October, the time of Hurricane Lili, may also have diminished the number of eggs available for survival. In addition, because the Exuma islands are on average much farther from potential lizard sources than are the Abaco islands considered here, recolonization would also be expected to be faster at the latter site.

The degree to which biotas are affected by major natural catastrophes has long been of ecological and biogeographical interest (*6*, *24–28*). Thanks to two temporally rare events, we now have obtained some idea of the range of recovery that is likely in an island system. In archipelagoes with more distant and less protected islands, such as the exposed Exumas just discussed, reconstitution by hatchlings is less likely and recolonization is less frequent. There the distribution of lizards may reflect the high-water mark of previous hurricanes over a sustained time (*16*). In contrast, when hurricanes strike early enough in the season and/or hit a sufficiently protected area, such as the Abaco site, lizard populations can survive in situ in the egg stage in great enough numbers to repopulate an island to its original level in about a year.

Our study provides extensive information on both natural extinction and natural restoration (*29*), topics of keen interest to conservation biology. Here, when the agent of mortality is a sudden inundating rise in sea level, altitude is more important than area in determining on which islands individuals are not drowned or washed away. However, the advantage of altitude is only temporary, lasting but a few months. Further recovery is more likely, the larger the island area. Three hypotheses may account for this eventual preponderance of area. First, the larger the area of an island, the larger the target for immigration of colonists. Such a target effect has been demonstrated in a variety of systems (*6*, *30*). Second, newly arrived colonists may find establishment easier on larger islands with more resources, and they will be able to attain larger population sizes on larger islands, favoring their persistence (*8–11*). Third, for islands reconstituted by egg survival, the larger the island, again the more resources and the greater the likelihood of successful development.

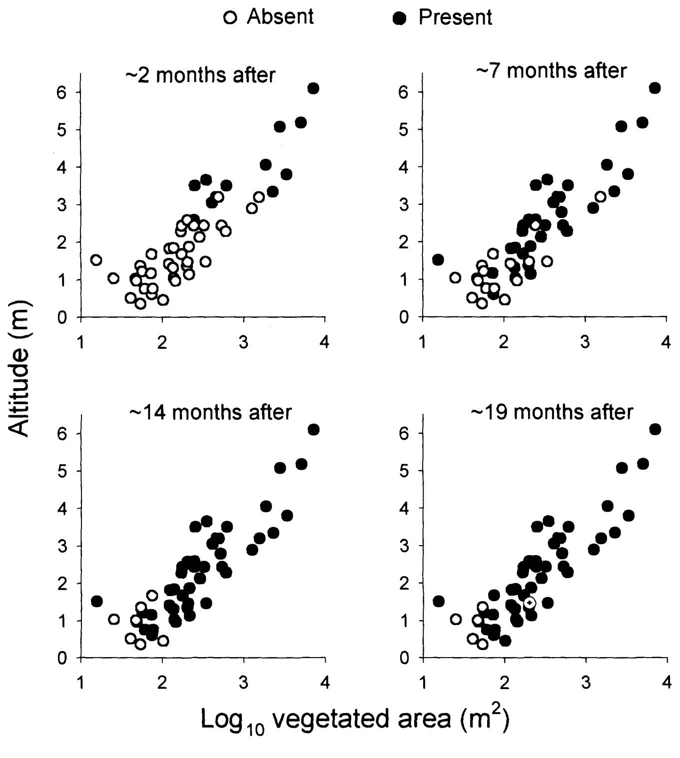

Fig. 3. Restoration of lizard distribution over the archipelago in relation to island area and altitude. Only islands found to naturally have *A. sagrei* before the hurricane are shown [see (*18*) for elaboration]. Adult or near-adult individuals were found on islands marked "present." Shortly after the hurricane (~2 months), such islands include most of the islands over 3 m high but are rather variable with respect to area. As time progressed, both lower and smaller islands were filled in, and area became a better and better predictor of which islands had lizard populations restored. At the end of the study, 19 months later, *A. sagrei* lizard populations that included adult or near-adult individuals were found on 88% of the islands, as compared to 24% of the islands immediately after the hurricane. The island marked with a cross in a circle (lower right panel) at ~19 months after the hurricane was the only island with a second species of lizard, the larger predatory *L. carinatus*. Sample sizes are as follows: ~2 months after the hurricane = 49 islands; on other dates = 50 islands.

In conclusion, although immediate survival from inundation relates to altitude, subsequent recovery relates to area, and ultimately it is area, not altitude, that is the better predictor of species occurrences. Thus, it is the distributional pattern over the entire archipelago, the species-area effect, that eventually recovers, not just populations on haphazard islands. In short, we have been provided with a rare glimpse of how nature can restore itself after a natural decimation.

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18. Before the hurricane (Fig. 1, top left), an island was classified as "absent": that is, not having lizards, if lizards were not seen there during the surveys of each of the previous 3 years (1999, 1998, and 1997). Otherwise, islands (without experimental introduction) were classified as "naturally present," except that if an island had lizards in 1997 (3 years pre-hurricane) but not in 1998 or 1999, it was classified as questionable and is not shown in the figure or included in the statistical computations of (*19*). Control islands for a previous experiment (*17*) were included, as was the island in that experiment naturally colonized by *L. carinatus*. If the last surveys were in 1995 or 1996 and lizards were seen, they were counted as present. Additionally, all unvisited islands exceeding 135 m^2 were inferred to have lizards before the hurricane, because no exceptions to this cutoff at the study site are known to us. After the hurricane (Fig. 1, remaining three panels), "absent" denotes no lizards seen, and "naturally present" denotes lizards seen and not founded by experimental introduction. An island classified as "introduced" has lizards according to the criterion for "naturally present" but received them in a single introduction in one of two previous experiments (*31*, *32*). Introduction islands having lizards from 1977 through 1996 and not visited since were also counted as "introduced."
19. "Area" is vegetated area and "altitude" is maximum elevation above the high-tide mark. Area is log-transformed; altitude is untransformed. For data without "introduced" islands, see (*18*), Score chi-squares give $P = 0.001$ ($\chi^2 = 10.782$) for log area and $P = 0.018$ ($\chi^2 = 5.624$) for altitude ($n = 59$ islands). Once log area is added, score chi-square for omission of altitude gives $P = 0.750$ ($\chi^2 = 0.102$). When "introduced" islands are

included ($n = 63$), the first two P values are 0.002 ($\chi^2 = 9.654$) and 0.022 ($\chi^2 = 5.276$), respectively, and the third $P = 0.587$ ($\chi^2 = 0.295$). The logistic procedure of SAS software was used for all computations.

20. None of the 65 such lizards exceeded 34 mm in snout-vent length, and only one other was larger than 31 mm. Maximum snout-vent length in *A. sagrei* in this region of the Bahamas is 57 mm for males and 44 mm for females.
21. For November 1999, score chi-squares for altitude and log area both give $P < 0.0001$ ($\chi^2 = 39.359$ and 28.758, respectively). Once altitude is added, score chi-square for log area gives $P = 0.328$ ($\chi^2 = 0.959$). For April 2000, score chi-squares for altitude and log area both give $P < 0.0001$ ($\chi^2 = 22.221$ and 21.259, respectively). Once altitude is added, score chi-square for log area gives $P = 0.151$ ($\chi^2 = 2.067$). For November 2000, score chi-squares for altitude and log area both give $P < 0.0001$ ($\chi^2 = 16.107$ and 22.856, respectively). Once log area is added, score chi-square for altitude gives $P = 0.135$ ($\chi^2 = 2.230$). For April 2001, score chi-squares for altitude and log area give $P = 0.0002$ ($\chi^2 = 13.632$) and $P < 0.0001$ ($\chi^2 = 19.195$), respectively. Once log area is added, score chi-square for altitude gives $P = 0.163$ ($\chi^2 = 1.948$). Introduction islands are included in all analyses.
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Role of Erv29p in Collecting Soluble Secretory Proteins into ER-Derived Transport Vesicles

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Proteins are transported from the endoplasmic reticulum (ER) in vesicles formed by coat protein complex II (COPII). Soluble secretory proteins are thought to leave the ER in these vesicles by "bulk flow" or through recognition by hypothetical shuttling receptors. We found that Erv29p, a conserved transmembrane protein, was directly required for packaging glycosylated pro-α-factor (gpαf) into COPII vesicles in *Saccharomyces cerevisiae*. Further, an Erv29p-gpαf complex was isolated from ER-derived transport vesicles. In vivo, export of gpαf from the ER was saturable and depended on the expression level of Erv29p. These results indicate that membrane receptors can link soluble cargo proteins to the COPII coat.

In eukaryotic cells, secretory proteins are packaged into COPII-coated vesicles at the ER for transport through the early secretory pathway. The mechanisms by which secretory proteins are segregated away from ER resident proteins during vesicle formation are still a matter of debate (*1*). Certain portions of integral membrane cargo appear to bind directly to subunits of the COPII coat (*2, 3*), allowing for their concentration into ER-derived vesicles (*4, 5*). It is less clear how soluble secretory cargos are exported from the ER, and evidence supporting bulk flow (*5*) and receptor-mediated export mechanisms (*2, 6*) exists. One difficulty with the receptor model has been the failure to identify integral membrane proteins that could fulfill this function.

In *S. cerevisiae*, COPII-coated vesicle formation has been reconstituted in cell-free reactions using ER membranes and purified COPII components: Sar1p, Sec23p complex, and Sec13p complex (*7*). COPII vesicles have been isolated and several of the abundant integral membrane constituents have been characterized in an effort to identify proteins involved in sorting during vesicle formation (*8*). One such ER-vesicle protein of 29 kD (hence Erv29p) is conserved across species (*9*), is selectively packaged into COPII vesicles (*8*), and contains multiple membrane-spanning domains with a terminal dilysine sorting signal (*10*).

Haploid *erv29Δ* strains are viable and display no observable growth defects (*8, 10*). To test whether *ERV29* deletion influenced protein transport between the ER and Golgi, we performed a reconstituted cell-free assay that measures transport of [^{35}S]gpαf to the Golgi complex (*11*). Surprisingly, no transport of gpαf was detected in membranes lacking Erv29p, although translocation of [^{35}S]pre-pαf into ER membranes was unaffected. Specifically, the defect in gpαf transport occurred at the COPII-dependent budding step. Budding of gpαf in wild-type membranes was efficient (33% of total), whereas only minor amounts (4% of total) were budded from *erv29Δ* membranes (Fig. 1A). To distinguish whether this result was due to a general decrease in COPII budding or a fail-

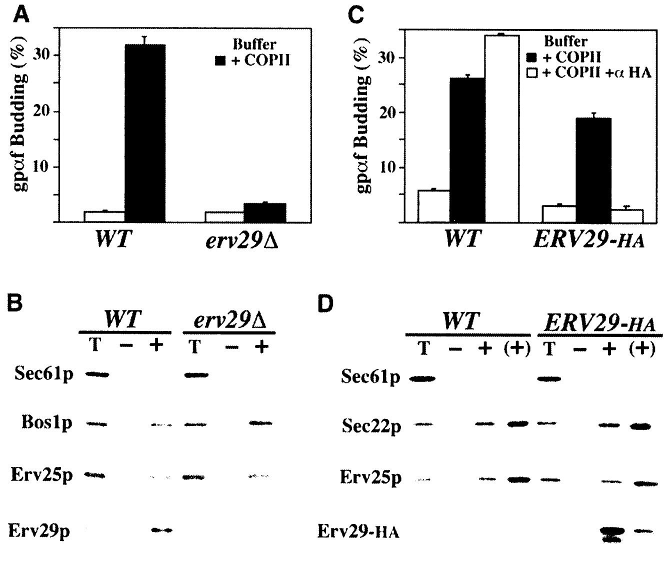

Fig. 1. Erv29p is required for gpαf packaging into COPII vesicles. Reconstituted COPII budding reactions from ER membranes isolated from FY834 (wild type, WT) and CBY966 (*erv29Δ*) are shown (*21*). (**A**) [^{35}S]gpαf budding reactions contained membranes incubated with or without purified COPII proteins (*7*). The percent budding represents the amount of [^{35}S]gpαf released in freely diffusible vesicles divided by the total amount of [^{35}S]gpαf contained in reactions. (**B**) Total membranes and budded vesicles, generated as in (A), were collected by centrifugation, resolved on polyacrylamide gels, and immunoblotted for the indicated proteins (*22*). Lanes labeled T represent one-tenth of the total; minus lanes show vesicles formed in the absence of COPII components; plus lanes show vesicles produced in the presence of COPII proteins. (**C** and **D**) As in (A) and (B), respectively, except that membranes from FY834 (WT) and CBY1160 (ERV29-HA) were used. HA mAb (0.07 mg/ml) was added to COPII budding reactions and is indicated by a bracketed plus sign (+) in (D).

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