both clones. The proliferative response to varying concentrations of HBsAg was also measured in the presence of a constant amount of antibodies to HBsAg. In the presence of antibodies to HBsAg (20 μg/ml), the maximum response to HBsAg could be achieved at antigen concentrations that were 1 to 10 percent of the concentrations required in the absence of the antibodies (Fig. 1, B and D).

In a separate experiment, we examined the effects of irrelevant antibodies—purified human antibodies to tetanus toxoid—on the HBsAg-induced proliferation of the helper T cell clones. The two T cell clones were specific for HBsAg and did not respond to tetanus toxoid (*5*). Antibodies to tetanus toxoid slightly inhibited the proliferative response (Fig. 2). The results indicate that the effect of antibodies to HBsAg on the T cell response to HBsAg is antigen-specific.

The exact mechanism by which the antibodies to HBsAg increase the response of the T lymphocyte clones to HBsAg has not been elucidated. One explanation is related to the ability of antibodies to polymerize and aggregate the antigen with which they react. The number of antigenic determinants or epitopes per molecule (valence) is higher in the polymer form, and this antigenic valence is directly proportional to the apparent binding affinity of the surface receptors for the antigen (*7*). One of us (E.C.) showed earlier that the binding of polyvalent antigen to solid phase–bound receptors can be regulated by soluble antibodies either competitively or synergistically, depending on the relative antibody concentration (*8*).

However, HBsAg and the antigen-antibody complexes probably do not bind directly to the antigen receptor on the T lymphocyte surface, and antigen-presenting cells such as macrophages and monocytes appear to play an important role in the antigen stimulation. Antigens aggregated by antibodies may be more easily captured than soluble antigens by these phagocytic cells. Additionally, the immunoglobulins in the immune complexes may bring them to the antigen-presenting cells through binding to the surface Fc receptors (*9*). The involvement of Fc receptors on monocyte interaction with immunoglobulins has been suggested in the studies of human T cell proliferation induced by monoclonal antibody OKT3 (*10*).

Our results suggest that antibodies may sustain or amplify normal immune responses in vivo by exerting the augmenting effects on T-helper cells. This positive-feedback effect of antibodies would most likely occur in secondary immune responses when some amounts of the specific antibody are already present in the circulation.

Several groups (*11*) have observed that antibodies to HBsAg are generated in some individuals given exogenous HBV-specific immunoglobulins. It was postulated that the small amounts of HBsAg present in some immunoglobulin preparations induced this "passive-active immunization" (*11*). Our results indicate that this suggestion may be correct since low concentrations of HBsAg become immunogenic when complexed with antibody to HBsAg, and an efficient immune response to HBsAg was observed in vitro even at high concentrations of antibodies (Fig. 1, A and C).

The role of antibodies in regulating immune responses in vivo has been studied by several groups. Although some reported that antigen-specific antibodies administered separately, or together with the immunogens, potentiate antibody responses (*12*), others found opposite results (*13*). The cellular mechanism responsible for these regulatory effects of antibodies has not been clearly characterized. Our present in vitro studies with helper T cell clones provide an explanation for some of the in vivo findings. It would be interesting to study whether the activities of antigen-specific T suppressor cells are also regulated by antibodies recognizing the same antigen and whether the opposing effects of antibodies in vivo are due to the unequal augmentation of helper and suppressor T cells.

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Ancient Ice Islands in Salt Lakes of the Central Andes

Abstract. *Massive blocks of freshwater ice and frozen sediments protrude from shallow, saline lakes in the Andes of southwestern Bolivia and northeastern Chile. These ice islands range up to 1.5 kilometers long, stand up to 7 meters above the water surface, and may extend out tens of meters and more beneath the unfrozen lake sediments. The upper surfaces of the islands are covered with dry white sediments, mostly aragonite or calcite. The ice blocks may have formed by freezing of the fresh pore water of lake sediments during the "little ice age." The largest blocks are melting rapidly because of possibly recent increases in geothermal heat flux through the lake bottom and undercutting by warm saline lake water during the summer.*

Between the eastern and western ranges of the Central Andes lies a broad, high basin of internal drainage known as the altiplano. Lake Titicaca is at the northern end, and Salar de Uyuni, a 9000 km^2 salt flat, dominates the central and lowest (3650 m above sea level) portion. At the southern end, the altiplano rises in elevation and is broken into a large number of small isolated basins, most of which contain one or more salt lakes (*1–3*). In ten of the several dozen lakes examined, we have found massive blocks of freshwater ice and frozen sedi-

ments projecting several meters above the water surface. These persist year-round and show little seasonal change.

The ten lakes with ice deposits are located at high elevations between 21° and 25°S and are all very saline and shallow (Fig. 1 and Table 1). Like the large salt lakes and salars of the central altiplano, these smaller basins contained deep, freshwater lakes at various times during the Quaternary (*1, 2, 4, 5*). At present, precipitation is between 50 and 200 mm per year and falls mostly during the summer months (December through February) as light rain or snow, with only occasional light snowfalls in the winter. Mean annual air temperature probably varies from about 0°C at the higher ice-containing lakes to 3° to 6°C at the lower ones. It is a cold desertic region.

The largest ice islands are in Laguna Colorada, Bolivia. In and around the margins of this lake are 10 to 25 km^2 of mud flats and salt crusts, depending on the season and year, and a little less than 1 km^2 of ice islands (Table 1). The lake's name derives from the bright orange color (Fig. 2, A and E), which is caused by a dense population of the flagellate *Dunaliella salina*. This and other algae also color the waters of other ice-containing lakes.

The most extensive ice islands, located in the center and in the northeast corner of Laguna Colorada, range up to 1.5 km long and stand up to 7 m above the water surface. The presence of ice usually is not obvious, for at all lakes the upper surfaces and sloped margins of the ice blocks typically are covered with 10 to 40 cm of whitish sedimentary materials of high albedo (Fig. 2, C and D). Aragonite or calcite is the principal material present, with various sulfates, borates, diatomaceous earth, organic matter, and volcanic ash occurring in lesser amounts or in particular situations; these same materials are common in the lake sediments and salar crusts of the region (*1–3*). The upper surfaces of the ice islands are hard-packed and may be gently undulating (Fig. 2C) or dissected by gullies, crevasses, and thermokarst and deflation basins.

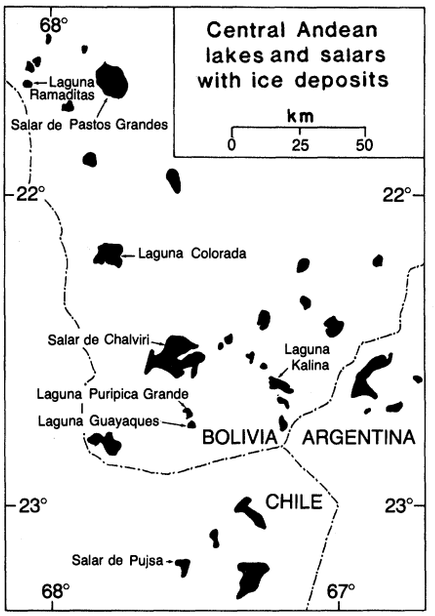

Fig. 1. Location in the central Andes of lakes and salars containing ice islands. Locations of lakes in Salar de Chalviri are shown in (*11*).

Only at rapidly wasting margins are the ice content and structure of the islands clearly displayed. The western and southwestern margins of the central ice islands (Fig. 2, A to D) in Laguna Colorada are especially exposed to marked wave action set up daily by strong afternoon winds from the west, southwest, or northwest. This wave action carries away the previously ice-bound sediments that otherwise accumulate in front of the ice islands (Fig. 2, D and E) and insulate them from the salt water, which at midday averages about 16°C in midsummer and 0°C in midwinter. The water then undercuts the ice so that large blocks break off, tilt into the lake, and melt. Reference stakes set in 1978 (Fig. 2E) indicate that the more exposed margins are retreating 10 to 15 m per year; elsewhere the wasting rates are much lower, often only centimeters per year.

The exposed faces of the central Laguna Colorada ice islands exhibit regular horizontal banding (Fig. 2, A and B). Strata of fairly pure freshwater ice up to 12 cm thick alternate with strata 10 to 35 cm thick containing frozen sediments in an irregular three-dimensional lattice of partitions of pure ice several millimeters thick (*6*). The ice-bound sediments are similar to materials on the upper surfaces of the islands. Elsewhere in Laguna Colorada, and at the other lakes, there is considerable variety in the relative amounts of ice and sediments and in the presence, regularity, number, and thickness of strata. Nowhere that we could observe are strata as numerous and regular as in the central islands of Laguna Colorada; but total ice content is just as

Table 1. Location and major features of ice-containing salt lakes in the Central Andes.

Lake or salar	Latitude (south)	Elevation (meters above sea level)	Area* (km^2)	Salinity† (per mil)	Mean water depth‡ (m)	Ice islands	
						Maximum height above water (m)	Areal extent (ha)
			Bolivia				
Laguna Ramaditas	21°38′	4117	4.1	28 to 38	0.1	3.5	1.5
Salar de Pastos Grandes	21°38′	4430	125	89	0.2	4.5	0.2
Laguna Colorada	22°10′	4278	50	60 to 292	0.2	7.0	80
Salar de Chalviri§			115				
Laguna Norte	22°28′	4388	7.0	78	0.2	1.5	0.1
Laguna Polques	22°32′	4393	12	13 to 17	0.2	0.7	1.0
Laguna Kalina	22°32′	4530	16	43 to 65	0.2	2.5	3.0
Laguna Puripica Grande	22°42′	4730	1.4	32 to 113	0.1	7.0	3.0
Laguna Guayaques	22°44′	4730	1.3	25 to 28	0.2	2.5	0.8
			Chile				
Salar de Pujsa	23°12′	4525	15	81 to 158	0.1	3.5	5.0
Salar de Aguas Calientes III	25°00′	3670	14	21	0.2	0.3	0.1

*Includes total of mud flats, salt crusts, and water, as their relative amounts vary markedly from year to year. †Ranges represent samples from different locations, different years, or both. ‡Values are approximate, perhaps high but are based on detailed inspection and refer only to areas with water. §This salar usually has about ten lakes, but only two contained ice. The locations are described by Hurlbert and Chang (*11*).

great at several of the other lakes, and at two of the highest ones, Laguna Guayaques and Salar de Pujsa, individual strata of almost pure ice 80 to 100 cm thick were observed.

To investigate the thermal conditions of the bottom of Laguna Colorada and to determine how far the ice deposits extend out beneath unfrozen lake sediments, we used a steel temperature probe 4 m long. At this lake the ice can extend considerable distances out from the above-water portions of the blocks—at least tens of meters in some locations, possibly hundreds of meters.

Temperature profiles through the top 3.5 m of lake sediment vary greatly from one part of Laguna Colorada to another and suggest high geothermal heat flux. Except within a few hundred meters of ice islands, sediment temperatures at 3.5 m range from 10° to 27°C and do not vary seasonally; the temperatures are highest near shoreline and sublacustrine thermal springs. Yet annual mean midlake water temperature is only about 4°C. Geothermal heat is apparently conducted upward over the entire lake bottom; this may explain the settling and fissuring observed for some ice-island margins completely protected from direct melting and erosion by lake water (Fig. 2F). The ice islands are not only wasting laterally but melting from below. Unless the high geothermal heat flux is a recent phenomenon, it is puzzling that the Laguna Colorada ice islands have persisted so long.

How long? Quechua Indians from villages 50 km to the east come and camp at the lake every summer (December through February) to harvest flamingo eggs. Individuals who first visited the lake in 1935 state that the ice was present then and always has been present as far as they and their parents ever knew. On a visit to the lake in 1924, Walcott (*7*) observed "salt deposits . . . seven or eight feet above the surface of the water," a presumably incomplete characterization and one similar to descriptions by modern geologists of the "salt hillocks" at Laguna Colorada, Laguna Ramaditas, and Salar de Pujsa (*2, 3*). Carbon-14 age determinations for the uppermost sediments in Laguna Colorada ice islands give an age of about 6000 years; the ice must be younger than the sediments incorporated in it. The uppermost sediments presumably were overlain, at the time of ice-island formation, by even younger sediments that have since eroded away.

The ice deposits at Laguna Colorada and most other lakes may have formed during the "little ice age," which affected most parts of the world, from the Middle Ages up to the end of the 19th century (*8*). But some are younger. The low-lying ice deposits in Laguna Polques formed sometime between our visits in February 1979 and January 1982 and have persisted through two summers. The smaller ice islands at Salar de Aguas Calientes, which we visited once in early summer (November 1975), were probably ephemeral formations.

The principal mechanism of ice-island formation may be the same as that by which massive ice beds and certain other lensed ice deposits form in and heave up river banks, delta soils, and drained lake bottoms on arctic coastal plains (*9*). Regardless of when the larger ice islands formed, the lakes were probably very shallow and saline, as they are now. The pore or interstitial water of the deeper sediments was presumably fresh, as it is now in Laguna Colorada (*10*), possibly left over from a deeper, freshwater phase of the lakes' history or originating from seeps and springs on the lake bottoms. Then when colder times arrived, the saline lake waters would not have frozen, would have given up their heat easily (even now water temperatures at Laguna Colorada drop to −6° to −7°C most nights in midwinter), and a freezing plane would have developed well below the sediment surface and penetrated downward. In such a situation water can be drawn up to the freezing plane from underlying sediments and form lenses or strata of relatively pure ice known as segregation ice (*9*). Thickness and frequency depend on freezing rate, availability of water beneath the freezing plane, and sediment particle size. The structural variety of the different ice islands is thus expected. The regularity of stratification in the central ice islands of Laguna Colorada (Fig. 2A) may reflect only the vertical homogeneity of sediment type one would expect in the center of the largest lake studied. The alterna-

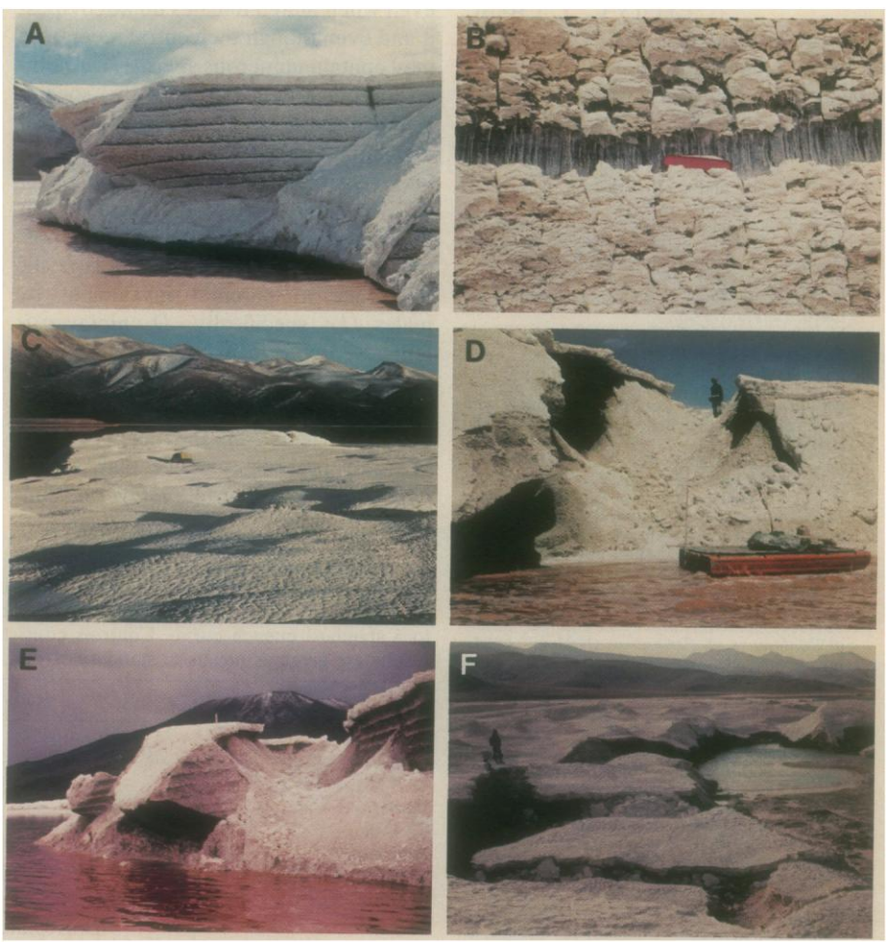

Fig. 2. Ice islands in Laguna Colorada, Bolivia. (A) Southwest margin of central ice island in winter (July 1980) showing stratification of ice and sediment. (B) Close-up of face in (A) showing 8-cm thick ice stratum. (C) Upper surface of central ice island (July 1980). (D) Large fissure in western headland of central ice island (January 1980). (E) Southwest margin of ice island with reference stake set in January 1978; at that time the stake on top of the calving block was 22 m back from the island margin, while in January 1982 when the picture was taken it was 1.5 m from the margin. (F) Slumping and fissuring along northern margin of central ice island (January 1982).

tion of segregation ice and frozen sediments may represent annual temperature cycles, although this type of stratification can also occur under constant temperature conditions.

Because formation of segregation ice involves drawing additional water into the system, and because segregation ice can continue to form even under great pressure, ice island heights of 7 m are not unexpected. At most lakes, the islands probably were even higher in the past and definitely were larger in area. These ice deposits are now disappearing, and the most spectacular ones, such as those at Laguna Colorada, will probably not persist for more than a decade or two. However, their future will be strongly influenced by even small changes in lake water level, air temperature, or geothermal activity.

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Drosophila Males Contribute to Oogenesis in a Multiple Mating Species

Abstract. *Two species of* Drosophila *that differ in their ecology and mating systems have been compared with respect to male contribution to the somatic tissues and developing oocytes of females. In the species* Drosophila mojavensis *females remate daily, exhibit a copulatory plug, and have been shown to obtain a contribution from the male ejaculate. In contrast,* Drosophila melanogaster *males do not contribute to females. Female* Drosophila melanogaster *do not remate as frequently as* Drosophila mojavensis *females nor is a copulatory plug formed.*

Species of *Drosophila* show wide variability in mating systems (*1*). One of the most striking differences observed is the frequency at which females of various species remate. For example, mated females of the cosmopolitan species *D. melanogaster*, when provided with males every morning, usually will not remate for about 5 to 7 days (*2*). Under similar conditions, females of the Sonoran Desert endemic cactiphilic species *D. mojavensis* remate daily. The pattern of daily remating in *D. mojavensis* is observed even when mated females do not oviposit and even though the ventral receptacle may contain numerous sperm (*1*). Another difference between these two species is the formation of a reaction mass or copulatory plug following mating in *D. mojavensis* but not in *D. melanogaster* (*3*). The evolutionary significance of this difference in remating frequency is postulated to be linked to an interspecific difference in parental investment by males (*1*); specifically, *D. mojavensis* females, living in a harsh environment often with limited resources, are predicted to remate more frequently in order to obtain nutrients from the male ejaculate. We now present evidence that, during copulation, males of *D. mojavensis* contribute nutrients to oocytes and to female somatic tissues while *D. melanogaster* males apparently do not.

Males were isotopically labeled by placing freshly oviposited eggs on Carolina instant *Drosophila* medium containing ^{3}H-labeled amino acids (*4*). Virgin males were separated upon eclosion and stored at 24° ± 1°C until they were required for mating experiments. After 4 days, labeled *D. melanogaster* males were mated to unlabeled females. Whole *D. melanogaster* males showed an average of 28,509 disintegrations per minute at the time of mating. Labeled *D. mojavensis* males were stored for 8 days before being mated to unlabeled females; these males showed an average of about 350,000 disintegrations per minute. The developmental time of *D. mojavensis* is 50 percent longer than *D. melanogaster*, which most likely accounts for the larger size of *D. mojavensis* and their higher concentration of radioactivity. The presence of isotope in mated females was determined immediately after copulation and again 24 hours later (*5*). The body parts analyzed are shown in Table 1.

In both species a large amount of radioactivity was seen in the female reproductive tract (uterus, ventral recepta-

Table 1. Radioactivity found in females at two times after mating. Data presented are averages for single females. At least three replications of three females per replication were performed for each time point. Counts per minute were converted to disintegrations per minute according to a standard quench curve. Controls consisted of body parts from unlabeled females. The results are given as means ± standard errors.

Part	Radioactivity (disintegrations per minute)		
	0 hours	24 hours	t*
	Drosophila melanogaster		
Head	18.9 ± 0.8	23.8 ± 6.1	1.39
Thorax	23.7 ± 4.6	31.1 ± 8.7	1.31
Abdomen†	39.5 ± 12.2	25.1 ± 3.1	1.09
Reproductive tract	1112.4 ± 63.1‡	50.4 ± 23.9	6.47§
Ovarian eggs	25.9 ± 9.8	23.9 ± 5.4	0.32
	Drosophila mojavensis		
Head	31.6 ± 6.6	56.23 ± 3.6‡	5.21‖
Thorax	50.4 ± 8.6	98.0 ± 5.5‡	7.77§
Abdomen	28.9 ± 6.4	72.2 ± 5.3‡	10.24§
Reproductive tract	1426.7 ± 118.6‡	67.4 ± 9.1‡	84.44§
Ovarian eggs	32.2 ± 8.5	191.7 ± 20.4‡	8.622§

*When appropriate, the Welch method was used (*11*); otherwise two-tailed t-tests were used to compare sample means. †Minus reproductive tracts. ‡Differs significantly from unlabeled controls. §$P < 0.01$. ‖$P < 0.05$.